HYDROBIOLOGIA

ACTA HYDROBIOLOGICA, HYDROGRAPHICA ET PROTISTOLOGICA

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Four numbers of the journal are published every year. Each number averages about 100 pages. Contributions must be clearly and concisely composed. They must be submitted in grammatically correct English, French, German, Italian or Spanish. Long historical introductions are not accepted. Protocols should be limited. Names of animals and plants must be given according to the laws of binominal nomenclature adopted at the recent International Congresses of Zoology and of Botany,

at the recent International Congresses of Zoology and of Botany, including the author's name; it is desirable that the latter should be given in full. Measures and weights should be given in the decimal system. Every paper has to be accompanied by a short summary, and by a second one, written in an alternative language.

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Groundwater Copepods from South-western Japan

by

TAKASHI ITO
(Limnological Laboratory, Faculty of Fisheries, Prefectural University of Mie, Japan)

(With 80 Text-figures and 14 Tables)

The present study is based on the copepod materials collected by Messrs. Yoshifumi Miura of Tatsuno High School, Yoshinobu Morimoto and Toshihiko Yokota of Himeji Municipal High School, from the thirty-one wells and two limestone caves in the southwestern parts of Japan as well as in the Island of Amami-Oshima.

Before going further, I wish to acknowledge my indebtedness to Messrs. Y. MIURA, Y. MORIMOTO and T. YOKOTA, who have kindly sent valuable materials for my use. I also wish to express many thanks to Dr. MASUZO UÉNO of the Otsu Hydrobiological Station, Kyoto University, for his kind advice on many matters. The present work was rendered possible through a scientific research grant from the Ministry of Education, to which I wish to express my sincere obligation.

LIST OF THE LOCALITIES AND THE SPECIES FOUND

The wells as the source of the waterworks of Aioi City, Hyogo Prefecture. (Collected by Y. MIURA).

No. 1: 2-VI-1953.

Paracyclops aioiensis n. sp. $1 \ \$; Acanthocyclops miurai n. sp. $1 \$; Diacyclops languidoides japonicus ITO $1 \$.

No. 2: 2-VI-1953.

Nothing.

No. 3: 20-VIII-1952.

Macrocyclops albidus (Jurine) 1 \circlearrowleft ; Acanthocyclops miurai n. sp. 2 \circlearrowleft , 1 \circlearrowleft .

No. 4: 20-VIII-1952.

No. 5: 10-IX-1953.

Macrocyclops albidus (JURINE) 1 2.

No. 6: 10-IX-1953.

Macrocyclops albidus (JURINE) 1 \cong .

The Chugoku district (Collected by T. YOKOTA)

No. 7: A well with pump; Karita-mura, Hiroshima Pref., W. T. 19.0° C, pH 5.8—6.1; 27-III-1954.

Diacyclops disjunctus (THALLWITZ) 2 ♀♀, 3 ♂♂; Diacyclops langui-

doides (LILLJEBORG) 1 9; Copepodid (Cyclopoida) 3.

No. 8: A well with pump; Yoshida-machi, Hiroshima Pref., W. T.

14.5° C, pH 6.2: 26-III-1954.

No. 9: A well with pump; Yoshida-machi, Hiroshima Pref., W. T.

14.5° C, pH 6.4; 18-VIII-1954.

Diacyclops languidoides japonicus ITO 3 \$\$, 13; Diacyclops languidoides suoensis ITO 1 5; Harpacticoida 1.

No. 10: A well with pump; Kamisugi-mura, Hiroshima Pref., 18-

VIII-1954. Ostracoda 15.

No. 11: A well with pump; Hamada City, Shimané Pref., 19-VIII-

1954. Diacyclops disjunctus (THALLWITZ) 1 3.

No. 12: A well with pump; Iwakuni City, Yamaguchi Pref., 23-VIII-1954. Eucyclops serrulatus (FISCHER) 18 \$\pi\$, 5 \$\frac{1}{2}\$; Acanthocyclops miurai n. sp. 1\$\pi\$; Diacyclops disjunctus (THALLWITZ) 1\$\pi\$; Copepodid (Cyclopoida) 1.

No. 13: A well with pump; Yamaguchi City, Yamaguchi Pref., 21-VIII-1954. Diacyclops disjunctus (THALLWITZ) 2 \$\$\,\text{2}\$, 1 \$\,\text{5}\$; Cope-

podid (Cyclopoida) 1.

No. 14: A well; Akiyoshi, Yamaguchi Pref., 22-VIII-1954.

Paracyclops fimbriatus (Fischer) 4 \$\pi\$; Diacyclops languidoides

(Lilljeborg) ?1 \$\frac{1}{2}\$; Mesocyclops leuckarti (Claus) 7 \$\pi\$\$.

No. 15: A pool in limestone cave "Shuhodo"; Yamaguchi Pref.,

22-VIII-1954. Mesocyclops leuckarti (CLAUS) 2 99.

Shikoku (Collected by Y. Morimoto)

No. 16: A well with pump; Ikeda-machi, Tokushima Pref., W. T. 18.0° C, pH 6.2; 25-VIII-1953.

Copepodid (Cyclopoida) 1.

No. 17: A well with pump; Akebono-cho, Kuma-machi, Ehimé Pref., W. T. 18.3° C, pH 6.2; 26-VIII-1953.

Eucyclops serrulatus (FISCHER) 1 ♀.

No. 18: A well with pump; Sugao, Kuma-machi, Ehimé Pref., W. T. 18.2° C, pH 6.2; 26-VIII-1953.

Eucyclops serrulatus (FISCHER) 1 \(\phi\); Diacyclops disjunctus (THALL-WITZ) 1 \(\phi\); Copepodid (Cyclopoida) 4.

No. 19: A pool in limestone cave "Ryugado"; Kochi Pref., 26-VIII-1953.

Eucyclops serrulatus (FISCHER) 3 99, 2 33; Microcyclops (Microcyclops) varicans (G. O. SARS) 2 33; Copepodid (Cyclopoida) 4.

Kyushu (Collected by Y. MIURA)

No. 20: A well; Sasaguri Station, Fukuoka Pref., W. T. 19.5° C, pH 6.1; 8-VIII-1954.

Thermocyclops uénoi ITO 1 \(\psi\); Copepodid (Cyclopoida) 3.

No. 21: A well; Sasaguri Station, Fukuoka Pref., W. T. 19.5° C, pH 6.1; 8-VIII-1954.

Eucyclops serrulatus (FISCHER) 1 \Im ; Diacyclops disjunctus (THALLWITZ) 2 \Im ; Thermocyclops uénoi ITO 15 \Im ; Copepodid (Cyclopoida) 2.

No. 22: A well; Seto-mura, Fukuoka Pref., W. T. 19.3° C, pH 6.1; 8-VIII-1954.

Diacyclops disjunctus (THALLWITZ) ? 2 33; Copepodid (Cyclopoida) 5.

No. 23: A well; Sasaguri-machi, Fukuoka Pref., W. T. 19.8° C, pH 6.0; 8-VIII-1954.

Diacyclops disjunctus (THALLWITZ) 1 ♀; 2 ♂♂; Copepodid (Cyclopoida) 10.

No. 24: A well; Araki Station, Fukuoka Pref.; W. T. 21.2° C, pH 5.8; 8-VIII-1954.

Eucyclops serrulatus (FISCHER) 4 ♀♀, 1 ♂; Copepodid (Cyclopoida) 1.

No. 25: A well with pump; Araki-machi, Fukuoka Pref., W. T. 21.7° C, pH 6.0; 8-VIII-1954.

Copepodid (Cyclopoida) 1.

No. 26: A well; Setaka-machi, Fukuoka Pref., W. T. 18.5° C, 8-VIII-1954.

Diacyclops disjunctus (Thallwitz) $2 \Leftrightarrow \varphi$, $1 \Leftrightarrow Diacyclops$ crassicaudis (G. O. Sars) $1 \Leftrightarrow Diacyclops$ languidoides (Lilljeborg) $7 \Leftrightarrow \varphi$, $4 \Leftrightarrow \vartheta$; Copepodid (Cyclopoida) 8.

No. 27: A well with pump; Hinagu-machi, Kumamoto Pref., W. T.

21.4° C, pH 7.4; 9-VIII-1954.

Halicyclops higoensis n. sp. 8 ♀♀, 1 0♂♂.

No. 28: A well; Hinagu-machi, Kumamoto Pref., W. T. 18.5° C, pH 6.6; 9-VIII-1954.

Copepodid (Cyclopoida) 2.

No. 29: An artesian well; Kitakawa-mura, Miyazaki Pref., W. T. 18.0° C, pH 6.4; 12-VIII-1954.

Eucyclops serrulatus (FISCHER) 1 3.

Island of Amami-Oshima (Collected by Y. MORIMOTO)

No. 30: A well with pump; Naze High School, Naze City; W. T. 24.0° C, pH 6.0; 12-VIII-1954.

Diacyclops disjunctus (THALLWITZ) 2 99, 1 3; Diacyclops languidoides suoensis ITO 1 9, 1 3; Copepodid (Cyclopoida) 3.

No. 31: A well with pump; Saiwai-cho, Naze City; W. T. 21.5° C, pH 6.4; 16 and 18-VIII-1954. Harpacticoida 3.

No. 32: A well with pump; Kariya-cho, Naze City; W. T. 21.2° C, pH 7.6; 18 and 19-VIII-1954.

Diacyclops languidoides suoensis ITO 1 3; Copepodid (Cyclopoida) 1; Harpacticoida 1.

No. 33: A well with pump; Saiwai-cho, Naze City; W. T. 21.8° C, pH 6.6; 18-VIII-1954.
Harpacticoida 1.

DESCRIPTION OF THE NEW FORMS AND REMARKS

1) Macrocyclops albidus (JURINE) (Table 1).

Length: Female 1.190 mm, Male 0.940 mm. Body white, without nauplius eye.

Occurence: No. 3 (1 \triangleleft); No. 5 (1 \triangleleft); No. 6 (1 \triangleleft).

Table 1. Macrocyclops albidus (JURINE)*)

	Furca (μ) Furcal seta i. : o. (μ)		Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: o. (μ)	Loca- lity
-	56:25 = 2.3:1	195:63 = 3.1:1	66:23 = 2.9:1	50:54 = 0.9:1	No. 3

^{*} i, inner; o, outer; L, Length; B, Breadth;

2) Eucyclops serrulatus (FISCHER) (Table 2)

Length: Female 0.868—1.277 mm, male 0.744—0.955 mm.

Body yellowish brown in colour, without nauplius eye.

(1 ♂); No. 24 (4 ♀♀, 1 ♂); No. 29 (1 ♂).

Table 2. Eucyclops serrulatus (FISCHER)

Furca (µ)	Furcal seta i. : ο. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: ο. (μ)	Loca- lity
$ \begin{array}{c} 142:26=5.4:1\\ 86:23=3.7:1\\ 135:26=5.1:1\\ 125:28=4.5:1\\ 112:23=4.9:1\\ 106:26=4.0:1\\ 86:21=4.0:1\\ 66:21=3.0:1\\ 106:25=4.3:1\\ 135:28=4.8:1\\ 109:23=4.7:1\\ 99:21=4.6:1\\ 102:23=4.4:1\\ 76:17=4.6:1\\ 109:23=4.7:1\\ 69:20=3.5:1\\ 73:17=4.4:1 \end{array} $	$\begin{array}{c} 99:63=1.6:1\\ 73:46=1.6:1\\ 106:79=1.3:1\\ 102:79=1.3:1\\ 88:66=1.5:1\\ 83:66=1.3:1\\ 86:50=1.7:1\\ 76:46=1.6:1\\ 109:73=1.5:1\\ 102:69=1.5:1\\ 79:66=1.2:1\\ 83:63=1.3:1\\ 83:63=1.3:1\\ 83:63=1.3:1\\ 92:46=2.0:1\\ 79:33=2.4:1\\ \end{array}$	73: 23 = 3.1:1 $56: 20 = 2.8:1$ $66: 30 = 2.2:1$ $66: 28 = 2.4:1$ $59: 26 = 2.3:1$ $59: 20 = 2.5:1$ $46: 20 = 2.3:1$ $59: 23 = 2.6:1$ $63: 26 = 2.4:1$ $53: 26 = 2.0:1$ $53: 26 = 2.0:1$ $53: 26 = 2.0:1$ $56: 23 = 2.4:1$ $43: 18 = 2.4:1$ $59: 26 = 23:1$ $56: 26 = 2.1:1$ $40: 20 = 2.0:1$	66:50 = 1.3:1 53:40 = 1.3:1 69:53 = 1.3:1 66:50 = 1.3:1 59:46 = 1.3:1 59:40 = 1.5:1 50:36 = 1.5:1 50:36 = 1.3:1 69:53 = 1.3:1 69:53 = 1.3:1 66:46 = 1.4:1 59:46 = 1.3:1 46:33 = 1.4:1 59:43 = 1.4:1 40:23 = 1.7:1	No. 8 ,,, No. 12 ,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,

^{*} with egg-sacs.

3) Eucyclops miurai ITO

Length: Female 0.828 mm, male 0.644 mm. Body white in colour, without nauplius eye.

Occurence: No. 4 (1 \circ , 1 \circ).

4) Paracyclops fimbriatus (FISCHER) (Table 3)

Length: Female 0.930—0.980 mm, body yellowish white in co lour. Nauplius eye entirely absent.

Occurence: No. 14 (4 99).

Table 3. Paracyclops fimbriatus (FISCHER)

Body- Length mm	Furca (μ)	Furcal seta i.: o. (µ)	Endopod 3, Leg 4 L. : B. (μ)	Spine, Endo- pod 3, Leg 4 i : ο. (μ)	1
,,0.942*	125:20 = 6.3:1 122:18 = 6.7:1 119:17 = 7.2:1	69:59=1.2:1	40:20 = 2.0:1 36:18 = 2.0:1 36:18 = 2.0:1	63:33 = 1.9:1 59:33 = 1.8:1 63:33 = 1.9:1	N

^{*,} with egg-sacs.

5) Paracyclops aioiensis n. sp. (Figs. 1—9; Table 4)

Female. — Length 0.608 mm except furcal setae. Body relatively flattened, yellowish brown in colour, without nauplius eye; abdominal segments not serrated except the last segment; anal incision fringed with marginal hairs.

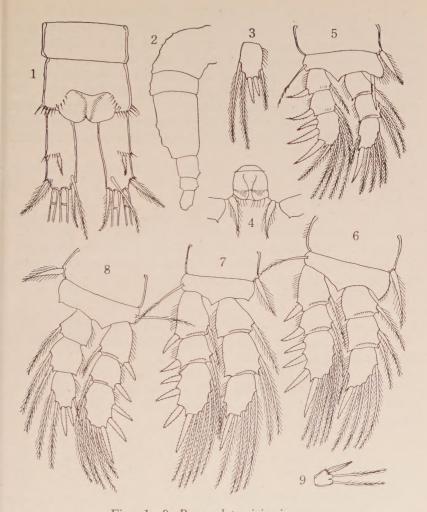
Furcal rami relatively short, 2.7 times as long as wide, slightly wide apart; lateral seta very small, inserted at distal 1/2.5, with a few transversely arranged denticles in front of the lateral seta on the dorsal surface; furcal setae well-developed, their length is, from inner to outer and dorsal, successively as follows:

Inner furcal seta a little longer than the outer (1.1:1), and a little longer than half the length of furcal rami; outer seta somewhat spine-like and shorter than the dorsal seta (Fig. 1).

First antenna markedly shorter than cephalothorax, consisting of 6 segments, the 3rd of which is very long (Fig. 2).

Table 4. Paracyclops aioiensis n. sp.

Body- Length mm	Furca Furcal seta i. : o. (μ)		Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: ο. (μ)	
9 0.608	63:23 = 2.7:1	36:33 = 1.1:1	28:20 = 1.4:1	26:20 = 1.3:1	1



Figs. 1—9. Paracyclops aioiensis n. sp.
Female, Aioi (Loc. No. 1), Hyogo Pref.
1. Furcal rami (dorsal); 2. First antenna; 3. Endopodite 3 of leg 4; 4. Connecting plate of leg 4; 5. Leg 1; 6. Leg 2; 7. Leg 3; 8. Leg 4; 9. Leg 5.

Connecting plate of Leg 4 is as shown in Fig. 4. Receptaculum

seminis not distinct.

Locality. — No. 1 (1 \circlearrowleft).

Holotype: Female (Loc. No. 1); the type is deposited in the Fa-

culty of Fisheries, Prefectural University of Mie.

Remarks: This species is distinguishable from *Paracyclops af-finis* (SARS) by the 6-segmented first antenna, the more longer inner furcal seta, the shorter inner terminal spine of the endopodite 3 of leg 4, and by the structure of legs 1—4 and 5.

6) Acanthocyclops miurai n. sp. (Figs. 10-19), Table 5)

Female. — Length 1.265 mm except furcal setae. Body white in

colour, without nauplius eye.

Furcal rami placed slightly wide apart, relatively short, 3.4 times as long as wide; inner margin without hairs; lateral seta located at about distal 1/3; furcal setae well-developed, their length is, from inner to outer and dorsal, as follows:

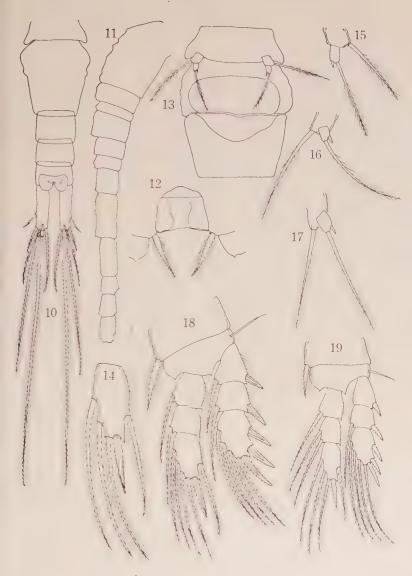
Loc. I II III IV V (in.) Aioi (Hyogo) 188 670 347 62 136
$$(\mu)$$

Inner furcal seta much longer than the outer (2.7:1), and longer than furcal rami (1.8:1); dorsal seta particularly well-developed, much longer than the outer seta, but shorter than the inner one.

Anal segment with a row of denticles on the dorsal surface of anal operculum (Fig. 10). First antenna consists of 12 segments, nearly reaching the end of cephalothorax (Fig. 11).

Legs 1—4: formula 3,3/3,3/3,3/3,3; spine-formula 2,3, 3,3; seta-formula 4,4, 4,4. (Figs. 18—21). Endopodite 3 of leg 4 reletively slender, twice as long as wide, bearing a single terminal spine, 42.9 μ in length; the terminal spine slightly shorter than the segment (81%); and the inner spine transforms into a long and slender, usual seta (Fig. 14).

Leg 5 consists of 2 segments; segment 1 larger and broad, with a



Figs. 10—19. Acanthocyclops miurai n. sp. Female, Aioi (Loc. No. 3), Hyogo Pref.

10. Abdomen and furcal rami (dorsal); 11. First antenna; 12. Connecting plate of leg 4; 13. Leg 5 and receptaculum seminis; 14. Endopodite 3 of leg 4; 15. Leg 5; 16. Leg 5; 17. Leg 5; 18. Leg 2; 18. Leg 4.

slender seta; seg. 2 small and slender, with a slender terminal seta and a small subapical spine (Fig. 13 and Figs. 15—17).

Connecting plate of leg 4 very simple, as shown in Fig. 12. Re-

ceptaculum seminis as shown in Fig. 13.

Male. — Length 1.004 mm. Body white in colour, nauplius eye entirely absent. Furcal rami about 3.9 times as long as wide. Both the inner and the dorsal furcal setae much longer than the outer one (2.7:1), and much longer than furcal rami (Fig. 22). Length of furcal setae is from inner to outer and dorsal, as follows:

Loc. I II III IV V (out.) Aioi (Hyogo) 125 533 298 46 99
$$(\mu)$$

Endopodite 3 of leg 4 reletively long, 1.8 times as long as wide, with a single terminal spine, and inner spine transforms into an usual seta as in female. (Fig. 23).

Type locality. — Aioi City, Hyogo Prefecture (Loc. No. 1, 1 $\stackrel{\circ}{\downarrow}$; Loc. No. 3, 2 $\stackrel{\circ}{\downarrow}$, 1 $\stackrel{\circ}{\circlearrowleft}$). The other locality (Loc. No. 12, 1 $\stackrel{\circ}{\downarrow}$).

Holotype. — Female; allotype: male (Loc. No. 3). The types are preserved in the Faculty of Fisheries, Prefectural University of Mie.

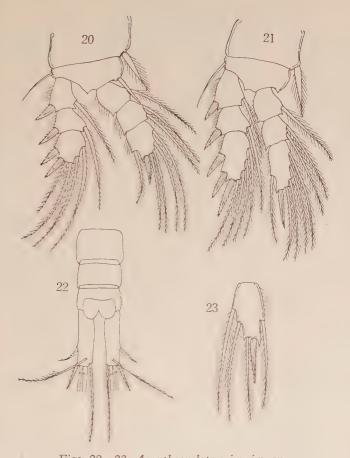
Variation. — The individual and local variations in some taxonomic characters of the new species are as shown in Table 5.

Table 5. Acanthocyclops miurai n. sp.

Body- Length mm	Furca (μ)	Furcal seta i. : o. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: ο. (μ)	
,, 1.265 3 1.004	102:30 = 3.4:1 89:23 3.9:1	$ \begin{vmatrix} 165:73 = 2.3:1\\ 188:69 = 2.7:1\\ 125:46 - 2.7:1\\ 185:46 = 4.0:1 \end{vmatrix} $	53:26 = 2.0:1 46:26 = 1.8:1	** 49.5 ** 42.9 ** 36.3 ** 52.8	

^{**,} The inner terminal spine transforms into a usual seta.

Remarks. — In its 12-segmented first antennae, longer inner and dorsal furcal setae, and formulae in legs 1—4, this new species is nearly allied to *Acanthocyclops morimotoi* ITO which was described by the author (1952) on the basis of specimens taken in the wells used for the water-works of Himeji City, Hyogo Prefecture. It is, however, distinguishable from *A. morimotoi* in the presence of a row of denticles on the dorsal surface of anal operculum and its inner terminal seta on endopodite 3 of leg 4.



Figs. 20—23. Acanthocyclops miurai n. sp. 20—21. Female; 22—23. Male; 20. Leg 1; 21. Leg 3; 22. Furcal rami (dorsal); 23. Endopodite 3 of leg 4.

Body- Length mm	Furca (μ)	Furcal seta i.: ο. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: ο. (μ)]
0.868 0.682 0.558 0.508 0.992 0.880 0.918 0.955 0.645 0.806 0.880 0.744 0.868 0.657 1.029* 0.769 0.620 0.645	69: 20 = 3.5: 1 53: 17 = 3.2: 1 46: 15 = 3.1: 1 40: 17 = 2.4: 1 79: 23 = 3.4: 1 73: 20 = 3.7: 1 63: 17 = 3.8: 1 83: 20 = 4.2: 1 76: 23 = 3.3: 1 69: 17 = 4.2: 1 69: 20 = 3.5: 1 79: 20 = 4.0: 1 79: 20 = 4.0: 1 69: 23 = 3.0: 1 56: 20 = 2.8: 1 79: 25 = 3.2: 1 66: 20 = 2.8: 1 56: 20 = 2.8: 1 56: 20 = 2.8: 1 56: 20 = 2.8: 1 46: 17 = 2.8: 1	36:30 = 1.2:1 $50:33 = 1.5:1$ $23:23 = 1.0:1$ $23:26 = 0.9:1$ $33:40 = 0.8:1$ $36:40 = 0.9:1$ $46:36 = 1.3:1$ $46:36 = 1.3:1$ $46:36 = 1.3:1$ $40:33 = 1.5:1$ $40:33 = 1.5:1$ $40:33 = 1.5:1$ $40:36 = 1.3:1$ $40:36 = 1.3:1$ $40:36 = 1.3:1$ $40:36 = 1.3:1$ $40:36 = 1.3:1$ $40:36 = 1.3:1$ $40:38 = 1.5:$	32:23 = 1.4:1 $26:20 = 1.3:1$ $23:17 = 1.4:1$ $20:15 = 1.3:1$ $36:26 = 1.4:1$ $30:20 = 1.5:1$ $36:26 = 1.4:1$ $30:20 = 1.5:1$ $36:26 = 1.4:1$ $30:23 = 1.3:1$ $30:23 = 1.3:1$ $30:23 = 1.3:1$ $30:20 = 1.5:1$ $36:26 = 1.4:1$ $30:20 = 1.5:1$ $36:23 = 1.3:1$ $36:23 = 1.3:1$ $36:23 = 1.3:1$ $36:20 = 1.5:1$ $36:23 = 1.6:1$ $30:20 = 1.5:1$ $36:23 = 1.1:1$ $26:23 = 1.1:1$ $23:20 = 1.2:1$ $26:23 = 1.1:1$	43:33 = 1.3:1 26:23 = 1.1:1 23:17 = 1.4:1 20:17 = 1.2:1 50:36 = 1.4:1 43:33	

*, with egg-sacs.

7) Diacyclops disjunctus (THALLWITZ) (Table 6)

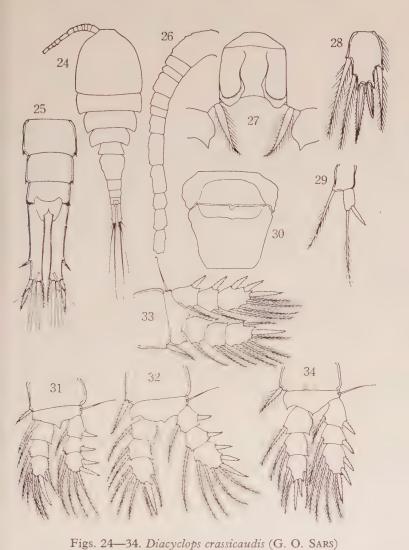
Length in mm: Female 0.868, male 0.508—0.682 (Loc. No. 7); female 0.880—0.992 (Loc. No. 8); male 0.694 (Loc. No. 11); female 0.918 (Loc. No. 12); female 0.955, male 0.645 (Loc. No. 13); female 0.744—0.880 (Loc. No. 21); female 0.868, male 0.657 (Loc. No. 23); female 0.942—1.209, male 0.781 (Loc. No. 26); female 0.620—0.769, male 0.645 (Loc. No. 30).

Body white in colour, nauplius eye entirely absent.

Occurence: No. 4 (1 $\,^{\circ}$); No. 7 (2 $\,^{\circ}$ $\,^{\circ}$ $\,^{\circ}$ 3 $\,^{\circ}$ 3); No. 8 (2 $\,^{\circ}$ $\,^{\circ}$ 9, 1 $\,^{\circ}$ 3); No. 11 (1 $\,^{\circ}$ 3); No. 12 (1 $\,^{\circ}$ 9); No. 13 (2 $\,^{\circ}$ 9, 1 $\,^{\circ}$ 3); No. 18 (1 $\,^{\circ}$ 3); No. 21 (2 $\,^{\circ}$ 9; No. 22 (2 $\,^{\circ}$ 3); No. 23 (1 $\,^{\circ}$ 9, 2 $\,^{\circ}$ 33); No. 26 (2 $\,^{\circ}$ 9, 1 $\,^{\circ}$ 3); No. 30 (2 $\,^{\circ}$ 9, 1 $\,^{\circ}$ 3).

8) Diacyclops crassicaudis (G. O. SARS) (Figs. 24—34, Table 7) Female. — Length 1.141 mm except furcal setae. Body white in colour, without nauplius eye.

Furcal rami very slender, 5.7 times as long as wide, placed relatively narrow together; lateral seta inserted at distal 1/4; inner margin



Female, Setaka (Fukuoka Pref.)

24. Female (dorsal); 25. Furcal rami (drosal); 26. First antenna; 27. Connecting plate of leg 4; 28. Endopodite 3 of leg 4; 29. Leg 5; 30. Receptaculum seminis; 31. Leg 1; 32. Leg 2; 33. Leg 3; 34. Leg 4.

13

without hairs; length of furcal setae is, from inner to outer and dorsal, as follows:

Loc. I II III IV V (out.) (dors.) Setaka (Fukuoka) 40 484 322 53 53
$$(\mu)$$

Inner furcal seta a little shorter than the outer (0.8:1), and markedly shorter than furcal rami (about 1/3); the dorsal seta nearly as long as the outer one, but longer than the inner seta. (Fig. 25).

First antenna consists of 12 segments, reletively short, not reach-

ng the end of cephalothorax (Figs. 24 and 26).

Legs 1—4: formula 3,3/3,3/3,3/3,3; spine-formula 2,3, 3,3; setaformula 4,4, 4,4. (Figs. 31-34). Endopodite 3 of leg 4 rather short, 1.2 times as long as wide; terminal spines markedly unequal, the inner spine much longer than the outer (1.8:1) and longer than the segment (125%). (Fig. 28). Connecting plate of leg 4 and receptaculum seminis are as shown in Fig. 27 and Fig. 30 respectively.

Leg 5 consists of 2 segments as shown in Fig. 29.

Occurence. — No. 26 (1 \circ).

Male. - Not collected.

Table 7. Diacyclops crassicaudis (G. O. SARS)

Body- Length mm	Furca (μ)	Furcal seta i. : o. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i : o. (µ)
\$1.141*	122:21 = 5.7:1	40:53=0.8:1	40:33 = 1.2:1	50:28 = 1.8:1

^{*,} with egg-sacs.

9) Diacyclops languidoides (LILLJEBORG) (Table 8)

Length in mm: Female 0.496 (Loc. No. 7); female 0.484 (Loc.

No. 8); female 0.583-0.744 (Loc. No. 26).

Body white in colour, without nauplius eye.

Occurence: No. 7 (1 \circlearrowleft); No. 8 (1 \circlearrowleft); No. 14 (1 \circlearrowleft); No. 26 (7 \circlearrowleft \circlearrowleft , 4 33).

Table 8. Diacyclops languidoides (LILLJEBORG)

Furca (µ)	Furcal seta i, : ο, (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i : ο. (μ)	Loca- lity
46: 15 = 3.1:1 40: 13	13:23 0.6:1 36:33 = 1.1:1 33:40 = 0.8:1	26:18 = 1.5:1	33:26=1.3:1	No. 7 No. 8 No. 14 No. 26

10) Diacyclops languidoides japonicus ITO (Table 9)

Length in mm: 0.794—0.843, male 0.682 (Loc. No. 8); female

0.893, male 0.707 (Loc. No. 9).

Body white in colour, nauplius eye entirely absent.

Occurence: No. 1 (1 $\stackrel{?}{\downarrow}$); No. 4 (4 $\stackrel{?}{\downarrow}$, 1 $\stackrel{?}{\circlearrowleft}$); No. 8 (11 $\stackrel{?}{\downarrow}$, 3 $\stackrel{?}{\circlearrowleft}$); No. 9 (3 $\stackrel{?}{\downarrow}$, 1 $\stackrel{?}{\circlearrowleft}$).

Table 9. Diacyclops languidoides japonicus Ito

Furca (µ)	Furcal seta i.: ο. (μ)	Endopod 3, Leg 4 L. : B.	Spine, Endo- pod 3, Leg 4 i. : ο. (μ)	Loca- lity
79:20 = 4.0:1 79:20 = 4.0:1 69:20 = 3.5:1 59:20 = 3.0:1 79:20 = 4.0:1 59:17 = 3.6:1	92:40 = 2.3:1 $96:43 = 2.2:1$ $86:40 = 2.2:1$ $66:30 - 2.2:1$ $76:36 = 2.1:1$ $76:30 = 2.6:1$	26: 23 = 1.1:1 $30: 23 = 1.3:1$ $23: 23 = 1.0:1$ $23: 20 - 1.2:1$ $33: 26 = 1.3:1$ $26: 20 = 1.3:1$	30: 26 = 1.1:1 $36: 33 = 1.1:1$ $28: 26 = 1.1:1$ $23: 20 - 1.2:1$ $33: 26 = 1.3:1$ $30: 26 = 1.1:1$	No. 8

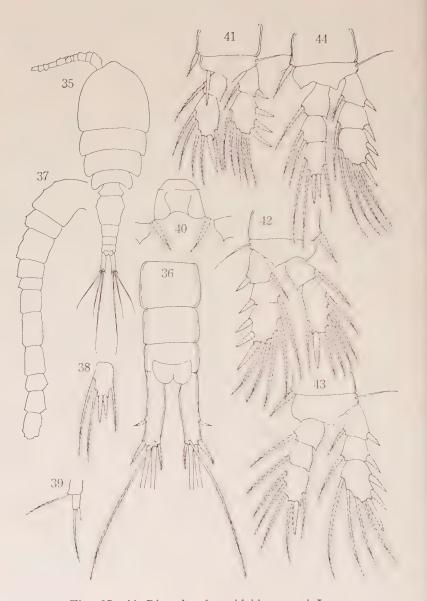
1) Diacyclops languidoides suoensis ITO

(Figs. 35-44, Figs. 45-48; Table 10)

Diacyclops languidoides suoensis, 1954, ITO, T., Report of Faculty of Fisheries, Prefectural University of Mie, Vol. 1, No. 3, p. 399—401, Figs. 144—148.

Male — Length 0.496 mm. (Loc. No. 9), 0.508 mm. (Loc. No. 32) except furcal setae. Body white in colour, nauplius eye entirely bsent.

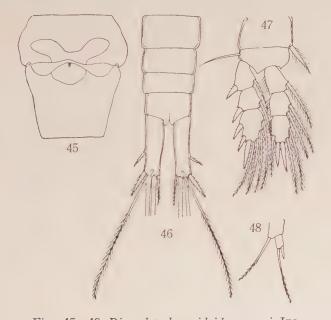
Furcal rami relatively short, 3.5—3.8 times as long as wide; ateral seta located at about distal 1/3; length of furcal setae is, from nner to outer and dorsal, as follows:



Figs. 35—44. Diacyclops languidoides sucensis ITO
Female, Naze (Amami-Oshima Island, Ryukyu).
35. Female (dorsal); 36. Furcal rami (dorsal); 37. First antenna; 38. Endopodite 3 of leg 4; 39. Leg 5; 40. Connecting plate of leg 4; 41. Leg 1; 42. Leg 2; 43. Leg 3; 44. Leg 4.

Loc.		I	II	III	IV	V	
		(in.)			(out.)	(dors.)	
Yoshida (Hiroshima)	(3)	17	372	119	20	102	(u)
Naze (Amami-Oshima)	(3)	23	273	136		112	(μ)
>>	(2)	20	248	124	23	132	(μ)
>>	(7)	26	260	124	26	139	(μ)

Inner furcal seta rather small, shorter than the outer (0.8-0.9:1), and also shorter than furcal rami (About 1/2); dorsal seta well-leveloped, markedly longer than furcal rami (about 2:1) and as long s the outer-median furcal seta. (Fig. 46).



Figs. 45—48. Diacyclops languidoides suoensis ITO
Naze (Amami-Oshima, Ryukyu).
15. Female, 46—48. Male. 45. Receptaculum seminis; 46. Furcal rami (venral); 47. Leg 4; 48. Leg 5.

Legs 1—4: formula 2,2/3,2/3,3/3,3; spine-formula 2,3, 3,3; setaformula 5,4, 4,4 as in *Diacyclops languiodides*, *D. languidoides japonicus*. Endopodite 3 of leg 4 very short, 1.2—1.4 times as long as wide; terminal spines nearly equal in length, the inner spine slighty longer than the outer one (1.2:1), and as long as the segment 100%). (Fig. 47). Leg 5 consists of 2 segments as shown in Fig. 48.

Female. — Length 0.570—0.657 mm. Body white, without nauolius eye.

Occurence. — No. 9 (1 \varnothing); No. 30 (11 \diamondsuit \diamondsuit , 1 \varnothing); No. 32 (1 \varnothing).

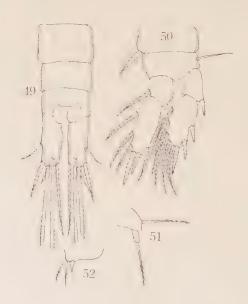
Table 10. Diacyclops languidoides suoensis ITO

Body- Length mm	Furca (μ)	Furcal seta i. : o. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i.: ο. (μ)
3 0.496 ♀ 0.570 ,, 0.620 ,, 0.645 ,, 0.657 3 0.508	46:13 3.5:1 50:17 = 3.4:1 53:15 = 3.6:1 53:15 = 3.6:1 56:15 = 3.8:1 56:15 = 3.8:1 50:13 - 3.8:1	17:20 0.8:1 20:23 = 0.9:1 20:23 = 0.9:1 23:23 = 1.0:1 26:26 = 1.0:1 23:26 = 0.9:1 23:26 0.9:1	20:17	20:17 - 1.2:1 23:17 = 1.4:1 23:20 = 1.2:1 23:20 = 1.2:1 26:21 = 1.2:1 26:20 = 1.3:1 23:20 1.2:1

12) Microcyclops (Microcyclops) varicans (G. O. SARS) (Figs. 49—52, Table 11)

Male. — Length 0.595—0.608 mm except furcal setae. Body yellowish white in colour, without nauplius eye.

Furcal rami nearly parallel, rather short, 2.6 times as long as wide; lateral seta inserted at distal about 1/3; inner margin without hairs; length of furcal setae is, from inner to outer and dorsal, as follows:



Figs. 49—52. Microcyclops (Microcyclops) varicans (G. O. SARS)
Male, limestone cave, "Ryugado" (Shikoku).
49. Furcal rami (dorsal); 50. Leg 4; 51. Leg 5; 52. Leg 6.

Loc. I II III IV V
(in.) (out.) (dors.)

Cave "Ryugado" (Kochi) 63 264 168 30 33 (
$$\mu$$
)

Inner furcal seta much longer than the outer (1.9—2.1:1); and onger than furcal rami; the dorsal seta slightly longer than the outer. (Fig. 49).

Legs 1—4: formula 2,2 2,2/2,2/2,2; spine-formula 3,4, 4,3; seta-formula 5,5, 5,5. Leg 4: exopodite 1 without inner seta; endopodite 2 relatively slender, with 3 setae on inner side, and a single seta on outer side, 2.3—2.5 times as long as wide; terminal spines unequal, the inner spine much longer than the outer (1.8:1), but narkedly shorter than the segment $(60-64^{\circ})$. (Fig. 50).

Table 11. Microcyclops (Microcyclops) varicans (G. O. SARS)

Furca (u)	Furcal seta i. : o. (μ)	Endopod 3, Leg 4 L.: B. (µ)	Spine, Endo- pod 3, Leg 4 i.: o. (µ)	Loca- lity
		46:20 = 2.3:1 50:20 = 2.5:1		

Leg 5 as shown in Fig. 51, similar to that of female. Leg 6: inner pine very small and short; outer 2 setae rather slender, nearly equal n length, and longer than the inner spine (Fig. 52).

Female. — Not found.

Occurence. - No. 19 (2 33).

3) Mesocyclops leuckarti (CLAUS) (Table 12)

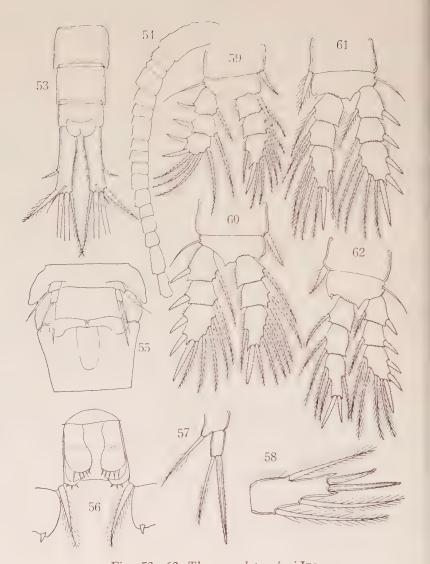
Length: Female 1.302—1.426 mm.

Body yellowish brown in colour, without nauplius eye.

Occurence: No. 14 (7 99); No. 15 (2 99).

Table 12. Mesocyclops leuckarti (CLAUS)

Furca	Furcal seta i.: ο. (μ)	i.: o. Leg 4		Loca-
(µ)		L.: B.		lity
2:33 - 3.1:1	310:109 = 2.8:1	89:33 = 2.7:1	76:83 = 0.9:1	No. 14
2:31 - 2.9:1	298:102 = 2.9:1	89:30 = 3.0:1	69:83 = 0.8:1	



Figs. 53-62. Thermocyclops uénoi Ito

Female, Sasaguri (Fukuoka Pref., Kyushu). 53. Furcal rami (dorsal); 54. First antenna; 55. Leg 5 and receptaculum seminis; 56. Connecting plate of leg 4; 57. Leg 5; 58. Endopodite 3 of leg 4; 59. Leg 1; 60. Leg 2; 61. Leg 3; 62. Leg 4.

(4) Thermocyclops uénoi ITO

Sas

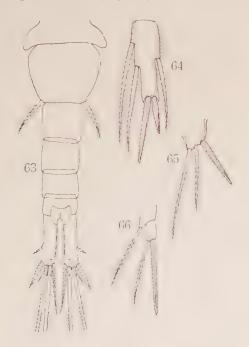
(Figs. 53—62, Figs. 63—66; Table 13)

Female. — Length 1.203—1.290 mm. Body brownish yellow in colour, nauplius eye entirely absent.

Furcal rami 3.4—4.1 times as long as wide; inner margin bearing 4 bundles of fine hairs; length of furcal setae is, from inner to outer and dorsal, as follows:

oc.			I	II	III	IV	V	
			(in.)			(out.)	(dors.)	
saguri	(Fukuoka)	(2)	112	434	310	79	66	(μ)
	,,	(2)	116	409	298	83	79	(μ)
	>>	(♀)	116	409	285	76	66	(μ)
	>>	(÷)	106	372	273	69	59	(μ)
	>>	(÷	116	372	298	79	73	(μ)
	22	(3)	83	360	248	46	76	(μ)

First antenna consists of 17 segments, relatively short, reaching to the end of cephalothorax (Fig. 54).



Figs. 63—66. Thermocuclops uénoi Ito Male, Sasaguri (Fukuoka Pref., Kyushu).

3. Abdomen and furcal rami (dorsal); 64. Endopodite 3 of leg 4; 65. Leg 6; 6. Leg 5.

Male. - Length 0.967 mm. Body brownish yellow, without

nauplius eye as in female.

Furcal rami nearly parallel in direction, 4 times as long as wide; lateral seta inserted at distal 1/3; inner margin with 4 bundles of fine hairs as in female; inner furcal seta longer than the outer (1.8:1), and slightly shorter than furcal rami; the dorsal seta longer than the outer, but shorter than the inner one. (Fig. 63).

Legs 1—4: formula 3,3/3,3/3,3/3,3; spine-formula 2,3, 3,3; seta-formula 4,4, 4,4 as in female. Endopodite 3 of leg 4 relatively slender, 2.6 times as long as wide; terminal spines unequal in length, the inner spine markedly longer than the outer one (1.7:1), and slightly shorter than the segment. (Fig. 64). Leg 5 as show nin Fig. 66. Leg 6 bearing a well-developed inner spine and 2 outer setae, the outer seta is longest. (Fig. 65).

Occurence. — No. 20 (1 ♀); No. 21 (15 ♀♀, 1 ♂).

	Table 13	. Thermocyclo	ps uénoi ITO
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Body- Length mm	Furca (µ)	Furcal seta i.: ο. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i : ο. (μ)	
,, 1.290 ,, 1.228 ,, 1.228 ,, 1.203	109:30 = 3.7:1 109:30 = 3.7:1 109:26 = 4.1:1 109:28 = 3.9:1	112:79 = 1.4:1 116:83 = 1.4:1 116:76 = 1.5:1 106:69 = 1.5:1 116:79 = 1.5:1 83:46 = 1.8:1	66:30 = 2.2:1 63:30 = 2.1:1 66:26 = 2.5:1 63:30 = 2.1:1	59: 40 = 1.5: 1 63: 43 = 1.5: 1 59: 43 = 1.4: 1 56: 40 = 1.4: 1 63: 43 = 1.5: 1 56: 33 = 1.7: 1]

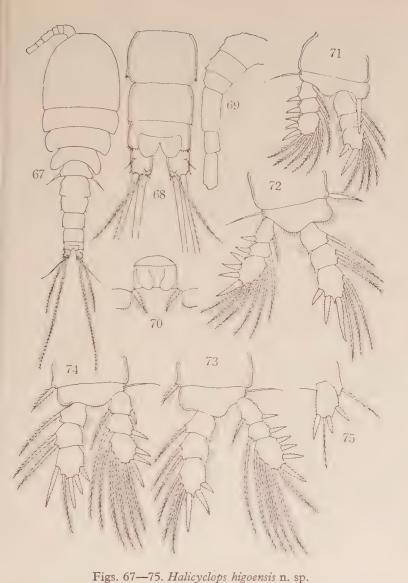
Remarks. — The present species was first described by the present author (1952) in the specimens from a well of Sashiki-machi, Kumamoto Prefecture, in the western part of Kyushu. The specimens of this locality had a distinctly red nauplius eye, but those collected from the wells in Sasaguri-machi, Fukuoka Prefecture, had no nauplius eye. Recently, I also found the blind forms in the specimens collected by Mr. Toshihiko Mizuno of Osaka Gakugei University from a well on the island "Tomogashima", Wakayama Prefecture.

15) Halicyclops higoensis n. sp.

(Figs. 67—75, Figs. 76—79; Table 14)

Female. — Length 0.521 mm except furcal setae. Body white in colour, nauplius eye entirely absent.

Anterior division of the body broad, somewhat flattened. Margins of abdominal segments smooth; lateral sides of the middle of genital



Female, Hinagu (Kumamoto Pref., Kyushu).
7. Female (dorsal); 68. Furcal rami (dorsal); 69. First antenna; 70. Connecting late of leg 4; 71. Leg 1; 72. Leg 2; 73. Leg 3; 74. Leg 4; 75. Leg 5.

segment slightly produced; anal segment generally deeply cleft ventrally, with a row of spinules at base of furcal rami. (Figs. 67 and 68).

Furcal rami very short, nearly as long as wide (1.1:1); inner and outer margins without hairs; lateral seta very small, inserted at distal 3/5. Length of furcal setae is, from inner to outer and dorsal, as follows:

Loc. I II III IV V (in.) (out.) (dors.) Hinagu (Kumamoto) 5 285 149 5 76 (
$$\mu$$
)

Inner and outer furcal setae very small and short, nearly equal in length, markedly shorter than furcal rami; dorsal seta very long, 3.8 times as long as furcal rami, and beset on a small protuberance; the inner-median seta very long, about twice as long as the outer-median seta; both median setae coarsely feathered. (Figs. 67 and 68).

First antenna consists of 6 segments, reaching to the middle of cephalothorax (Figs. 67 and 69). Second antenna consists of 3

segments.

Legs 1—4: formula 3,3/3,3/3,3/3,3; spine-formula in exopodite 3,4,4,3; seta-formula in exopodite 5,5,5,5; spine-formula in endopodite 2,3,3,4; seta-formula in endopodite 4,3,3,1. Endopodite 2 of leg 1 bearing a single seta, but those of legs 2—4 with 2 setae respectively. Endopodite 3 of leg 4 rather short, nearly as long as wide (1.2:1); terminal spines unequal in length, the inner spine longer than the outer one (1.3:1), and also longer than the segment (114%); the outer marginal seta spine-like, 13μ in length; the proximal inner marginal seta also spine-like, 33μ in length. (Figs. 71-74).

Leg 5: segment 1 fused with the last thoraxic segment, and bears a slender seta; segment 2 is a flat plate, with 3 short spines and a slender seta. (Fig. 75). Connecting plate of leg 4 as shown in Fig. 70.

Male. — Length 0.459 mm. Body white in colour, without nauplius eye as in female.

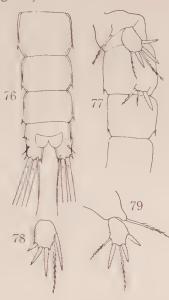
Furcal rami very short, as long as wide (1.0:1); length of furcal setae is, from inner to outer and dorsal, as follows:

Loc. I II III IV V (in.) (out.) (dors.) Hinagu (Kumamoto) 3 235 112 3 56
$$(\mu)$$

Both inner and outer setae very small, equal in length; the dorsal seta rather long, 3.4 times as long as the furcal rami.

Formulae of legs 1—4 similar to those of female. Endopodite 3 of leg 4 rather short, oval in general outline, 1.2 times as long as wide; the terminal spines unequal in length, the inner spine longer than the outer one (1.6:1), and a little longer than the segment (114°) ; outer marginal and inner proximal setae transforms into a

spine as in female, 11.6μ and $26,4 \mu$ in length respectively (Fig. 78). Leg 5 with 3 short spines and 2 slender setae (Fig. 79). Leg 6 bears a stout inner spine and 2 outer setae, the outermost seta longer than the median seta (Fig. 77).



Figs. 76—79. *Halicyclops higoensis* n. sp. Male, Hinagu (Kumamoto Pref., Kuyshu).

76. Furcal rami (dorsal); 77. Leg 5 and 6; 78. Endopodite 3 of leg 4; 79. Leg 5.

Type locality. — Hinagu-machi, Kumamoto Prefecture, Kyushu. (Loc. No. 27, 8 ♀♀, 10 ♂♂).

Holotype. — Female; allotype: male (Loc. No. 27). The type are deposited in the Faculty of Fisheries, Prefectural University of Mie.

Variation. — The individual variation in some taxonomic characters of the present species from the type locality are as shown in Table 14.

Table 14. Halicyclops higoensis n. sp.

Furca (μ)	Furcal seta i. : o. (μ)	Endopod 3, Leg 4 L. : Β. (μ)	Spine, Endo- pod 3, Leg 4 i : ο. (μ)	Loca- lity
20:17 = 1.2:1 20:18 = 1.1:1 20:18 = 1.2:1 17:17 - 1.0:1	5:5 = 1.0:1 5:5 = 1.0:1 4:4 = 1.0:1 3:3 - 1.0:1	23:23 = 1.0:1 23:20 = 1.2:1 23:20 = 1.2:1 23:20 = 1.2:1	26:20 = 1.3:1 $26:20 = 1.3:1$ $26:20 = 1.3:1$ $26:17 - 1.6:1$	No. 27

Remarks. — This new species is allied to both *Halicyclops neglectus* Kiefer and *H. rotundipes* Kiefer. The former was reported by Kiefer (1935, 1936) and Schäfer (1936) from the brackish-water regions in Holland, Belgium, England and Hiddensee. The latter was described by Kiefer (1935, 1936, 1938a, 1938b) from the Bulgarian coast of the Black Sea and the Korfu Island. This new species is also the closest to *H. rotundipes putealis* Kiefer, which was reported by Kiefer (1938b) from the brackish- and fresh-water wells in Bari City, South Italy. It is, however, distinguishable from the above-mentioned three forms in having the very short, spine-like inner and outer furcal setae, the spine-like inner proximal seta of endopodite 3 of leg 4, and the more selender leg 5.

AN ABNORMAL FORM

An abnormal male of *Eucyclops serrulatus* (FISCHER) was collected from a well in Iwakuni City, Yamaguchi Prefecture, Western Japan. The furcal rami of this animal are remarkably asymmetrical; the left



Fig. 80. Abnormal form in furcal rami of *Eucyclops serrulatus* (FISCHER). Iwakuni (Yamaguchi Pref.)

ramus is normal, 2.6 times as long as wide, but the right one is very long and slender, 6.8 times as long as wide, without the inner- and the inner median-setae, the outer seta markedly long, seta-like, about

twice as long as the left one. However, the other characters are normal (Fig. 80).

SUMMARY

In this paper the following 15 groundwater species belonging to the Cyclopoid Copepoda are reported, which were collected in 33 localities, 31 wells and 2 limestone caves, in various districts in Southwestern Japan, such as Chugoku, Shikoku, Kyushu and the Ryukyu Islands.

Wells: Macrocyclops albidus (JURINE)

Eucyclops serrulatus (FISCHER)

Eucyclops miurai ITO

Paracyclops fimbriatus (FISCHER)

Paracyclops aioiensis n. sp.

Acanthocyclops miurai n. sp.

Diacyclops disjunctus (THALLWITZ)

Diacyclops crassicaudis (G. O. SARS)

Diacyclops languidoides (LILLJEBORG)

Diacyclops languidoides suoensis ITO

Mesocyclops leuckarti (CLAUS)

Thermocyclops uénoi ITO

Halicyclops higoensis n. sp.

Subterranean pools in limestone caves:

Microcyclops (Microcyclops) varicans (G. O. SARS) ("Rūygadō", Kochi Pref., Shikoku)

Mesocyclops leuckarti (CLAUS) ("Shūhōdo", Yamaguchi Pref.).

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The distribution of sulphur in the muds, water and vegetation of Lake Victoria

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INTRODUCTION

An article by BEAUCHAMP (1953) suggests that a sulphur shortage in Lake Victoria is a factor limiting the growth-rate of fish. It has been demonstrated in the laboratories of the East African Fisheries Research Organisation (Fish, 1956) that a shortage of sulphate in the lake water is controlling the growth-rate of phytoplankton and, phytoplankton being the main source of nutrients for *Tilapia* sp. which is the fish of greatest economic value, this apparent sulphate

deficiency is a problem of primary importance.

Owing to the fact that sulphates are removed from the water by biological precipitation in the form of animal and plant remains, BEAUCHAMP suggested that the sulphate ultimately becomes anaerobically reduced to insoluble and unavailable sulphides which accumulate in the mud of the lake bed. Thus, although the water is deficient in sulphur the element may well be present in large quantities at the bottom of the lake. It was subsequently shown (HESSE, 1956) that although sulphur was indeed present in abundance in the bottom deposits of the lake, it was not in the expected form of sulphide but in organic combination.

The East African Fisheries Research Organisation records (1954) show that the species of *Tilapia* such as *T. zillii* which feed on higher plants have a higher growth-rate than those feeding on phytoplankton. This suggests that the higher plants contain more nutrients than does

phytoplankton.

In order to obtain facts as to the amounts of sulphur in the waters, muds and vegetation of Lake Victoria a preliminary investigation was undertaken in the northern area around Jinja. Water, mud and vegetation samples were taken from Napolean Gulf, Pilkington and Thruston bays, Roseberry and Buvuma channels and from the open

lake, and soils were collected from several of the numerous small islands in the area (Fig. 1).

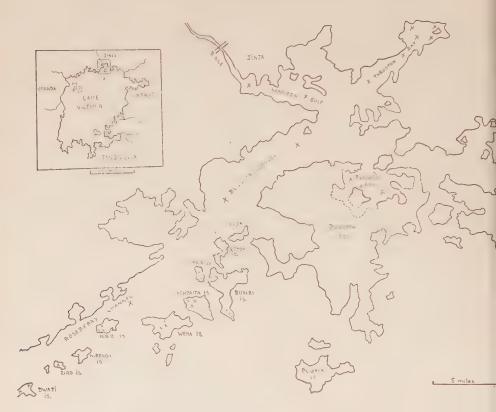


Fig. 1. Sketch map of part of Lake Victoria showing sampling sites.

METHODS

- 1. Sampling: Water samples were collected from various depths with a Rutner-type water sampler. Surface muds were obtained with a Jenkins apparatus (MORTIMER, 1942) and the deeper muds with a peat borer.
- 2. Sulphur Analyses: Sulphate-sulphur, organic-sulphur, sulphide-sulphur and total sulphur were measured. All the forms with the exception of sulphide were ultimately measured as sulphate by the method described by Chesnin & Yien (1950). The sulphate-sulphur in the muds and soils was extracted with Morgans' reagent using a ratio of one part mud to five parts solution. The sulphate in the plants was extracted by shaking the finely divided

material with very dilute hydrochloric acid and activated carbon, a special standard graph being used for the calculations. Using the apparatus described by SMITTENBERG et al (1951) sulphides were decomposed, with hot concentrated hydrochloric acid and the liberated hydrogen sulphide measured iodimetrically. Total sulphur in the vegetation, muds and soils was determined as sulphate after oxidation with a perchloric-aqua regia mixture and in the water after oxidation with nitric acid and bromine. All traces of nitrate were removed by repeated evaporation with hydrochloric acid and any yellow colour due to ferric chloride was conveniently removed with metallic zinc as ferrous iron is not co-precipitated with barium sulphate. Organic-sulphur in the muds was determined as sulphate after oxidation with hydrogen peroxide and in the water and vegetation by calculation from the measured total and sulphate contents.

3. Other Analyses: The following determinations were made by routine methods: pH, moisture, silica, carbon, nitrogen, ferrous and ferric iron, manganese, dissolved oxygen and oxidation-reduction potentials. The redox potentials were measured the day after collection, the muds having been stored in completely filled bottles kept under water in the dark. Potentials measured whilst on the boat immediately the samples were obtained were very little different from those measured the next day.

RESULTS

1. Water Samples

The analytical results are shown in Table 1 and as far as the area examined is concerned, verify Beauchamp's statement that the waters of Lake Victoria are deficient in sulphur. The sulphate content was less than one part per million in all samples and the total sulphur content rarely exceeded one part per million. These figures may be compared with those for Lake Edward which contained fifteen parts per million sulphate-sulphur and forty parts per million total sulphur in its surface water. By concentrating large volumes of water from the surface of the open lake the absolute quantities of sulphur present were found to be 0.18 p.p.m. SO₄-S and 0.38 p.p.m. total-S.

The rainwater collected on shore at Jinja contained 0.01 p.p.m. SO_4 -S and 0.08 p.p.m. total-S which for an average rainfall of fifty inches corresponds to an annual deposition of 0.9 lbs. total-S pre arce.

During the investigation (March-May) the water at all depths and

at all stations was found to be highly oxygenated. Unpublished data obtained by FISH however, show that oxygen depletion of the deep (60 metre) water in the open lake can occur between the months of February to April.

TABLE I

The analyses of water samples from Lake Victoria
(Percent oxygen saturation has been corrected for height of 3700 ft. above sea level)

Site	Depth	Temp.	0_2 mg/l	% 0 ₂ saturation	pН	p. _I total	p.m. S sulphate
Napolean Gulf	Surface	26.5	6.86	99.5	8.2	1	< 1
North Buvuma	Surface	27.1	6.90	100.0	8.3	1	< 1
Channel	10 m	26.2	6.87	99.5	8.3	0.5	<. 1
	15 m	26.2	5.20	75.5	8.2	1	< 1
	20 m	26.2	4.28	62.1	8.0	0.5	< 1
South Buvuma	Surface	26.1	6.82	98.9	8.2	1	< 1
Channel	5 m	26.1	6.53	94.6	8.2	1	< 1
	15 m	26.1	6.21	90.1	8.0	0.5	< 1
	25 m	25.8	6.22	90.2	7.9	0.5	< 1
Roseberry	Surface	26.3	6.59	95.3	8.1	1	< 1
Channel	5 m	25.8	6.38	92.4	8.1	1	< 1
	15 m	25.6	5.11	74.2	8.1	2	< 1
	25 m	25.6	4.60	66.7	8.0	2	- 1
Open Lake*	Surface	25.3	6.91	100.0	8.2	0.4	< 1
0°.04′ south	10 m	25.3	6.92	100.0	8.2	0.3	< 1
33°.00′ east	20 m	25.3	6.87	99.5	8.0	0.3	< 1
	30 m	25.2	6.64	96.2	7.9	0.5	< 1
	40 m	25.2	6.50	94.1	7.8	0.5	< 1
	50 m	25.1	6.16	89.3	7.8	0.6	< 1
	59 m	25.0	4.98	72.1	7.6	0.7	< 1
Pilkington	Surface	26.2	7.16	100.0	8.9	1	< 1
Bay*	1 m	26.2	7.03	100.0	8.9	1	< 1
	2 m	26.1	7.13	100.0	8.9	0.5	< 1
	3 m	26.0	7.14	100.0	8.9	0.5	< 1
	4 m	26.0	6.76	97.9	8.9	1	< 1
	5 m	26.0	6.83	99.0	8.7	1	< 1
	6 m	26.0	6.83	99.0	8.6	1.5	< 1
	7 m	26.0	6.76	97.9	8.6	1	< 1
Thruston	Surface	26.6	7.11	100.0	8.2	1	< 1
	0.5 m	26.6	6.92	100.0	8.2	1	< 1
	1.0 m	26.6	7.10	100.0	8.2	0.5	< 1
	1.5 m	26.6	6.95	100.0	8.2	0.5	< 1
	2.0 m	26.6	6.95	100.0	8.2	0.5	< 1

^{(*}Oxygen measurements made by Dr. J. F. TALLING, University of Khartoum)

mdd	50 106 107 107 107 107 107 107 107 107 107 107	0	100
mdd	60 50 180 240 240 200 189 140 278 270 276 29 58	10 10 24 68 128 268 306 424 424 540	780 700 155 700 190 190
mdd	5806 5913 5740 7274 5000 3015 3165 4910 5830 4390 6340 9510	240 9110 7011 8128 8224 5160 8128 8907 9728 8738	11420 16020 10035 8930 1090 1090
mdd	5911 6004 5947 7601 5284 3228 3400 5225 6170 4717 6405 9566	9167 6981 8296 8400 5448 8068 9527 10146 9432	12600 16800 10200 9640 1222 1222
% %	26.5 8.00 19.6 3.82 21.7 5.47 13.2 3.12 18.5 2.29 10.4 1.48 11.7 0.79 12.2 0.83 10.1 1.31 10.8 0.62 7.4 0.51 2.8 0.50		12.3 1.94 14.4 2.38 n.d. n.d. 14.1 2.19 12.4 1.62 12.4 1.62
%	7 1.710 0 0.025 8 nil 3 nil 3 0.028 1 0.050 1 nil 7 nil 7 nil 7 0.050 8 0.017		0.025 0.030 0.025 0.454 0.454
% %	1.77 1.47 1.60 0.60 0.50 0.50 0.50 0.50 0.50 0.50 0		1.68 1.56 1.01 1.35 n.d. 1.02 0.85 1.86 15.87 2.91 15.87 2.91
% Au	6.8 440 10.5 6.7 150 15.3 6.5 100 16.1 6.5 96 18.9 6.4 71 16.7 6.5 67 12.1 6.6 139 25.4 6.6 139 25.4 6.6 111 47.2 6.5 140 46.3 6.6 145 48.5 6.7 130 56.4 1	282 20.0 230 19.4 108 23.7 121 36.8 176 43.7 166 48.7 163 52.1 110 60.4 60 61.8	6.2 350 41.2 6.2 339 40.4 6.4 310 n.d. 3 6.0 340 36.9 6.9 403 70.2 12 6.8 58 70.2 12
%	98.1 97.8 97.8 97.3 97.3 97.3 97.5 76.5 76.5 79.2 79.2 79.2	97.5 96.4 96.0 93.8 86.8 71.8 66.9 57.2	95.0 96.7 78.1 96.4 87.6 87.6
pnu	0—3 cm 3—10 cm 0.1—1.0 m 1.0—3.0 m 4.0—4.5 m 5.5—6.0 m 7.0—7.5 m 9.0—9.2 m 9.2—9.5 m 11.5—12.0 m 13.0—13.5 m	0-3 cm 3-10 cm 0.1-1.0 m 1.0-2.0 m 2.0-3.0 m 3.0-4.0 m 4.5-5.0 m 5.0-6.0 m	0.0—0.5 m 0.0—0.5 m 0.0—0.5 m 0.0—5 cm 5.0—50 cm
water	ш 6	e H	30 m 30 m 20 m 16 m 60 m
	Pilkington Bay	Thruston Bay	Roseberry Channel S. Buvuma Channel N. Buvuma Channel Napoleon Gulf Open Lake (0°—04′ south) 33°—00′ east)

2. Mud Samples

Some typical results are given in Table 2 and have been calculated where necessary to an oven-dry basis. The pH values were very constant and approached neutrality at all depths from the mud surface to fifteen metres. This was in contrast to the water which in every case was distinctly alkaline. Iron was present in both the oxidised and reduced states and the redox potentials indicated a condition more on the oxidising side than the reducing. In the Pilkington Bay profile ferric iron had accumulated in certain strata and in some cases its concentration rose as high as 15—17%. Sulphur was present in abundance mostly in the organic form. Silica formed a large percentage of the total weight of the muds but varied in its form: for exam-

TABLE 3

The analysis of aquatic plants from Lake Victoria

Site	Plant	Sulphur Total	as % S Sulphate		% Nitrogen	% Ash
Pilkington	Papyrus head	0.069	0.032	0.037	1.54	6.5
Bay	Papyrus stem	0.032	0.027	0.005	0.60	7.3
	Papyrus roots	0.138	0.035	0.103	1.66	8.8
	Waterlily leaves	0.112	0.037	0.075	3.54	9.2
	Waterlily stem	0.038	0.018	0.020	1.18	19.9
	Hydrilla verticilata Ceratophyllum	0.186	0.040	0.146	2.42	11.6
	demersum Potamotagen	0.276	0.123	0.153	2.78	16.4
	schweinfurthii Phytoplankton	0.126	0.046	0.080	1.96	2.0
	(60% diatoms) Phytoplankton	0.248	nil	0.248	3.00	39.6
	(85% diatoms) Phytoplankton	0.017	nil	0.017	n.d.	n.d.
	(98% diatoms)	0.084	nil	0.084	n.d.	n.d.
	Pistia sp. leaves	0.306	0.241	0.065	1.92	21.0
	Pistia sp. roots	0.712	0.556	0.156	1.40	18.4
	Echinochloa sp. leaves		0.009	0.043	2.22	6.0
	Echinochloa sp. stems	0.140	0.140	trace	0.98	8.2
Thruston	Papyrus head	0.087	0.003	0.084	1.80	5.1
Bay	Papyrus stem	0.067	0.016	0.051	0.60	7.9
	Papyrus root	0.094	0.031	0.063	1.18	7.1
	Waterlily leaves	0.136	0.019	0.117	3.34	0.8
	Waterlily stem Ceratophyllum	0.078	0.017	0.055	1.14	13.4
	demersum	0.178	0.109	0.069	2.06	3.0
	Water chestnut	0.204	0.130	0.074	2.04	10.4

ple, in the mud of Thruston Bay the silica was mostly as sand whereas that from Pilkington Bay was mostly accounted for by diatom frustules (BEAUCHAMP, priv. comm.).

3. Vegetation

The analytical results are shown in Table 3. All the aquatic plants contained appreciable amounts of sulphur, the overall, average content being 0,1%, a value comparable to that for wheat and grass. The form in which the sulphur occured was variable; for example, in the stems of *Echinochloa* practically all the sulphur was as sulphate whereas in the leaves of the same plant the sulphur was mainly in the organic form. The two samples of *Papyrus* also had different organic-sulphur/sulphate-sulphur distributions and presumably the variable relative proportions represent different stages in the biology of the plants.

It is of interest that the plant containing most sulphur was the water-cabbage (*Pistia* sp.) which floats in the water and is not rooted in the lake bed. The sulphur content of phytoplankton was variable.

4. Island Soils

The analytical results are given in Table 4. There were patches of natural forest on most of the islands and in every case the soil from these forests contained sulphur. The sulphur was present almost entirely in the organic form but as the soil was sampled to only 30 cm it is possible that sulphate-sulphur was present at greater depths as has been found under forests in other parts of East Africa (Hesse 1955). Apart from the forest regions the island topsoils were very low in sulphur content. This sulphur shortage was particularly marked on the stony hilltops with poor vegetation, the low-lying areas near the lake shores containing rather more of the element. The southern part of Busiri Island was well covered with grass and trees and its soil contained far more sulphur than those of the other islands. The only large concentration of sulphate-sulphur found was in the soft, upper layer of a sheet ironstone deposit on the shore of Yemonita Island.

DISCUSSION

The outstanding fact arising from the analyses of the lake muds is the very low sulphide content. It had been expected that the muds would be rich in sulphur but it was thought that the element would be mainly in the form of ferrous sulphide. In actual fact only about -4% of the total sulphur present was in the reduced form even at

TABLE 4

The sulphur contents of soils from islands in Lake Victoria

Island	Site	Depth	Total-S	p.p.m. S Organic-S	Sulphate-S
Vuga	Hilltop, stony	06"	0	0	0
		6—12″	30	30	0
	Saddle between	0—6"	0	0	0
3.71 1.	two hills	6—12" 0—6"	0 140	140	0
Nienda	Forest on hilltop	6—12"	215	215	0
	Stony hilltop	0-6"	85	85	. 0
	otony mitop	6—12″	45	45	0
Sindiri	Forest	0-6"	283	275	8
		6-12"	182	170	12
	Beyond forest on	0-6"	125	125	0
	higher ground	612"	89,	80	9
Busiri	South point, open	0-6"	400	395	5
	parkland	6—12″	500	500	0
	South point,	0—6"	440	440	0
	banana plantation	6—12″	275	275	0
	Forest	0—6"	435	435	0
	Classed match in	6—12″	500	500	0
	Cleared patch in	0—6" 6—12"	515	515 575	3
Yempaita	forest Lake shore, grass	06"	578 140	575 140	0
Temparta	Lake shore, grass	612"	35	35	- 0
	Lake shore, shallow	0-4"	125	125	0
	soil over murram	4—12″	1200	0	1200
	Forest	0—6"	245	245	0
		6—12"	175	175	0
	Hilltop, stony	0—6"	0	0	0
		6—12"	10	10	0
Wema	Hilltop, stony	0—6"	0	0	0
	FT: 4 0	612"	17	0	17
	Thin forest	06"	50	50	0
	T at a set a second	6—12″	80	80	0
	Lake shore, grass	0-6"	0	0	0
Kibibi	Hilltop, stony	6—12" 0—6"	40	40	0
KIDIDI	Timop, stony	6—12"	95 0	95 0	0
	Flat plain above	0—12	20	20	0
	forest	6—12"	0	0	0
	Forest	0-6"	285	285	0
		612"	110	110	Ö
	Lake shore	06"	115	115	0
		6-12"	237	237	0
Kirengi	Very little soil extremely rocky	0—4″	0	0	0
Ziro	Very little soil	0—6"	40	40	0
Dwaji	South point,	0—6″	382	382	0
,	forest	6—12″	30	30	0
	South point, grass	0—6"	128	0	128
		6—12″	10	10	0
	South point,	06"	0	0	0
	hilltop, stony, some grass.	6—12″	50	50	0

depths of fifteen metres below the mud surface. This low sulphide content together with the comparatively high sulphate values, the presence of ferric iron and high redox potentials seemed to indicate that anaerobic conditions do not exist to any great extent at the lake bottom.

Additional evidence of the oxidised state of the muds was inferred from the fact that although the muds contained appreciable amounts of sulphate as extracted by Morgans' reagent, the water filtered from those muds was practically devoid of sulphate. For example, the top 3 cm of mud in Pilkington Bay contained 60 p.p.m. SO₄-S yet the water in contact with it contained less than 1 p.p.m. This phenomenon has also been observed by KOYAMA & SUGARAWA (1951) in the mud of certain Japanese lakes and by using radioactive sulphur they subsequently showed (1952) that ferric iron complexes in the flocculent mud sorbed sulphate ions from the lake water. The classic experiments of MORTIMER (1941) have demonstrated that complexes in oxidised muds adsorb sulphate and other anions. Furthermore, reduction of such muds brings about the breakdown of the sorbing complexes with the resultant liberation of ions to the associated water.

Experiments similar to those of MORTIMER were carried out using Lake Victoria muds. These experiments did not give the expected results and are being described and discussed in another paper. However, it may be said here that a straight forward adsorption of sulphate by ferric complexes is not entirely responsible for the lack of exchange of sulphate between mud and water as previously thought.

CONCLUSION

The bottom deposit of the lake is a highly fertile material and is rich in nutrients. It has been mooted at Jinja that mud should be pumped up from the lake bed and used to reclaim swamp-lands nearby, but in order that the organically bound nutrients should be available the mud would have to be induced to decompose.

Apart from any adsorption process that may occur, sulphates are removed from the lake water biologically in the formation of plankton and other vegetable matter. This organic material for the most part is eventually deposited on the lake bed where it accumulates. Thus as stated by Beauchamp, one of the limiting factors in the fertility of the lake is the rate of decomposition of the bottom deposits. As shown by the results in Table 2, the mud even at depths of ten to fifteen metres below its surface, that is, material probably laid down several thousands of years ago, is highly organic in nature. Also, as over

ninety percent of the total sulphur in the muds is in organic combination, it would appear that the rate of decomposition of the bottom deposits is extremely slow and is probably the most important factor limiting the concentration of nutrients in the lake water. An investigation into the rate and mode of decomposition of Lake Victoria muds and of factors affecting their decomposition has been made and will be described in another paper.

The aquatic plants of the lake contain ample sulphur for their needs. In certain cases such as that of *Pistia* sp., where the plants float with trailing roots they help to remove sulphur from the lake to the mud where, as will be discussed in a future paper, not only will the organic sulphur remain unoxidised but the sulphate may either become converted to organic forms or fixed in some other manner.

Sulphate in the soils of the islands is rapidly leached away and would eventually reach the lake unless it is held by the forest regions or, as on Yempaita Island, by an impenetrable layer of rocky material. Very little sulphur is supplied to the lake via the rain and the sulphur demands of the aquatic fauna and flora must be met principally by the inflowing streams.

SUMMARY

The sulphur contents of the muds, water and vegetation at the northern end of Lake Victoria have been determined. Contrary to previous assumptions it was found that the sulphur in the bottom deposits is principally in the form of organic compounds and not as sulphides. Evidence is presented which suggests that the muds are in an aerated condition. The water of the lake contains extremely small amounts of sulphur and receives a negligible quantity of this element from the rain. The soils of the islands in the lake are rocky and well-leached of sulphur except where patches of forest conserve it. Certain peculiarities were noted in the behaviour of the muds and these are to be discussed in a future paper.

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Succession of marine fouling organisms on test panels immersed in deep-water at la Jolla, California

by

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This work was undertaken with the view that no special study has been made on the succession of marine fouling organisms on artificial substrata immersed in deep water. On the other hand, extensive work has been published on the settling of such organisms on various test panels at or near the water surface in different areas, particularly in connexion with experiments on antifouling paints. A comprehensive survey of such work was prepared by Woods Hole Oceanographic Institute in the U.S.A. (1952).

While fouling organisms are considered as a nuisance to ships, buoys and other floating structures, as well as to pilings in harbours, they may cause serious inefficiencies to sound devices, electronic units, cables and other instruments intended for under water research.

It is assumed that the fouling community differs in quantity and in quality both with depth as well as with distance from the shore; light seems to play an important rôle in limiting the growth of certain such organisms.

The aim of the present experiment, is to find out whether there is a biological succession of the fouling organisms in deep water, at least during the early stages of the fouling process, comparable to the sequence established for these organisms at the surface or in shallow water by some authors. In this respect we must distinguish between two different problems in the study of the biology of fouling, which have often been confused, viz:

a) Ecological succession in the sense applied to the land community or to denuded rock surfaces colonized by algae and animals on the sea shore, and which may ultimately lead to a climax.



ig. 1. Lowering the experimental cage supporting the test panels into the sea.

b) Periodical or seasonal variations in the amount of the settling organisms.

MATERIAL AND METHODS

The experiment was undertaken in the coastal waters off the Scripps Institution of Oceanography at La Jolla, from the end of March through June 1955, i.e. during 12 weeks. Other obligations, unfortunately, did not allow the extention of observations beyond

this period.

A metallic cage (fig. 1) constructed of a galvanized iron sheat to which frames of iron piping were electrically welded, served as a support for the test panels. The sheat measures 6 feet (180 cm) × 4 feet (120 cm) and a 1 inch (6 mm) thick. Three transverse girdles of thick wire were thus welded to the four corners of the cage at distances of 25" (63 cm), 313" (79 cm) and 39" (99 cm) successively from the base; and these were installed with loops for the attachment of the test panels. The latter consist of slates of glass, plexiglass, vinyl acetate, wood, beside thin metallic sheats of iron, stained steel, zinc, brass and copper in various convenient dimensions and numbers. All these substrata were new and not previously treated with sea water. They were attached to the cage, in different directions, by nylon string or thin wire.

The cage supporting the panels was lowered with winch from the end of the Scripps Pier into a motor-boat, whereby it was sunk into a sandy bottom at a depth of 45 feet (ca 14 m) below mean sea level and at a position of about 400 yards (364 m) from the shore; in the mean time being at about 1 mile (1.6 km) away from the nearest Kelp bed in the region. Such conditions ensure a more random chance for the settling organisms and, as will be shown later, it was not necessarily the organisms found in abundance in the littoral region during the experiment which settled, but a rather distinct succession was manifested.

The cage was so designed as to lie stable on the bottom through its own weight without being seriously disturbed by bottom currents and waves.

The panels were tested in situ by means of diving with a Cousteau-Gagnan aqualung and a full dress, made of foamed-rubber for protection, since the temperature at the bottom was of the order of 12°C. One or two dives a week were made at the beginning of the experiment, later a dive every fortnight was made. Observations were recorded underwater on vinyl acetate slates, while samples or whole panels for microscopic examination were taken whenever desired. Such a method of investigation ensures protection of the test panels and does not disturb the sequence of the settling organisms, nor does it permit contamination by other growths as is usually the case with panels which are raised mechanically to the surface and lowered again each time an examination of the fouling organisms is made.

CONSIDERATION OF THE FOULING COMMUNITY

In this paper the marine fouling community is treated as a dynamic unit or as a working mechanism in the sense of ALEX. WATT (1947), i.e. starting with a pioneer phase, the community grows changing in time and space until a "climax" is reached. The stages which give the community a characteristic pattern at any given time are here called "phases" and these are defined by the dominant organism whether it be an animal or a plant.

The word "phase" had previously been used by Huvé (1953) to describe ecological succession, but he also uses "associations" to describe the "ensemble" of populations of different organisms, adding that these associations represent different phases of the succession and consequently the fouling community comprises several such associations.

Other workers e.g., Sheer (1945) use the word communities for phases which we here consider only as temporal stages in the fouling mechanism.

A consideration of the interrelations of the successive phases is given in the discussion to follow.

RESULTS

The panels were suspended at about 1 or 2 feet (0.3—0.6 m) above the bottom. The intensity of colonization varies greatly according to the direction of exposure and type of substratum. Even on the same panel the distribution of one or more of the organisms may be irregular or contageous. However, in almost all cases, the quality and sequence of the major settling organisms appear to follow a certain definite succession. This succession is manifested by the following phases. Lagging of any one phase among the different substrata or overlapping of phases is not unlikely. An example of such successive phases on plexiglass panels is reproduced in fig. 2.

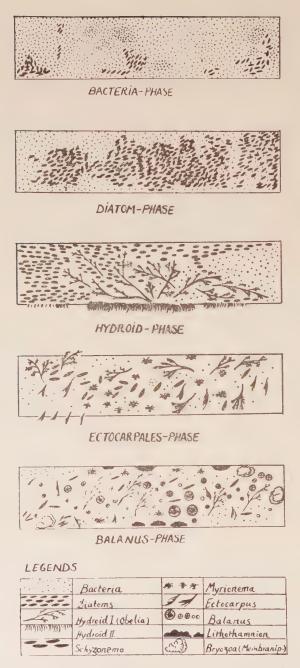


Fig. 2. Diagrammatic representation of succession phases on plexiglass panels.

1. BACTERIA - PHASE

Within the first few days a bacterial film invariably appeared on most of the test panels, with the exception of the copper slates, and to a less extent on brass, zinc and stained steel.

The heaviest film of bacteria was noticed on plexiglass, with a maximum deposition on the surface directed to the inside of the cage (protected side). The bacteria involved were mostly cocci and bacilli and were firmly adhering to the surface.

cilli and were firmly adhering to the surface.

By the end of the first week, a faint brownish film of diatoms appeared towards the edges of plexiglass panels, already covered with bacteria and such diatoms were more evident later on in the follow-

ing phase.

Most of the earlier workers (e.g. WILSON 1925, COE & ALLEN 1937) seem to have overlooked this bacterial phase as the initial phase of colonization of substratum by marine organisms and consider the diatoms as the pioneer phase. However, ZOBELL & ALLEN (1935) drew attention to the rôle of bacteria in this respect.

2. DIATOM-PHASE

As previously mentioned this phase starts towards the end of the first week of immersion, at first as a few scattered individuals of motile pennate diatoms, which multiply to form a film bound to the substratum by mucous secretions. Those pennate naviculoid diatoms belonging to the genus *Schizonema* (*Navicula*), later on secrete gelatinous tubes inside which they arrange themselves and multiply so as to give the appearance of branched filaments, often obscured with filamentous brown algae like *Ectocarpus*.

The following diatoms were detected from faint brown films on

plexiglass panels:

Pleurosigma normani (f)

Schizonema (Navicula) ramosissima (f)

Navicula spp. (f)

Cocconeis scutellum (f-c)

Grammatophora marina (f)

Nitzschia pandorina (r)

Coscinodiscus excentricus (p,r)

(c, common; f, frequent; r, rare; p, planktonic).

Together with the diatom film, the dinoflagellate *Prorocentrum* micans Ehr. was observed in abundance. This species was responsible, later on, for the red water at La Jolla during April, 1955.

Scratching the surface of glass or plexiglass is apparently without

effect on the density of colonization of diatoms. Wood comes next to plexiglass or glass in sustaining a well developed diatom film, then come the metallic surfaces, which supported diatoms in different degrees by the end of the second week of immersion.

A Protozoa "subphase" seems hardly separable from this diatom phase, since along with the diatoms and bacteria, a few ciliates and amoebae were detected. Such protozoa, often brousing on diatoms and bacteria fit well in this biotope and the relation between the two is undoubtedly one of food requirements.

Since their appearance on the different substrata during these early stages, the bacteria, diatoms and protozoa have been detected also in subsequent phases and seem to reproduce several generations.

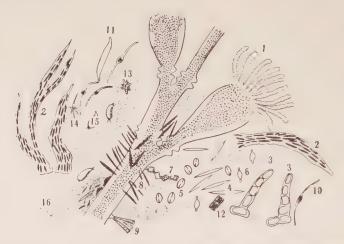


Fig. 3. Details of the fouling community on plexiglass after 2 weeks immersion 1. Obelia dichotoma; 2, Schizonema (Navicula) ramosissima (colonial diatom in gelatinous tubes); 3, Ectocarpus-sporling; 4, Nitzschia sp.; 5, Cocconeis scutellum; 6, Amphora sp.; 7, Striatella unipunctata; 8, Synedra tabulata; 9, Licmophora abbreviata; 10, Nitzschia closterium; 11, Pleurosigma normani; 12, Grammatophora marina; 13, Amoeba sp.; 14, Amoeba (radiosa stage); 15, a ciliate protozoan; 16, Bacteria.

By the end of the second week, the following organisms, apart from protozoa, have been distinguished on different panels, particulary on the opaque vinyl acetate slates and on plexiglass (fig. 3) (a, abundant; c, common; f, frequent; r, rare).

Diatoms:

Schizonema ramosissima (covers 20 % of glass and plexiglass surfaces; 80 % of wood). Licmophora abbreviata (f) Climacosphenia moliniger (f)

Grammatophera marina (f) Cocconeis scutellum (c)

Navicula spp. (f)

Gomphonema spp. (f)

Dimerogramma minor (r)

Pleurosigma normani (f)

Amphora spp. (f)

Synedra spp. (f)

Nitzschia closterium (r)

N. pandorina (f)

Melosira spp. (r)

Coscinodiscus excentricus (r, p)

C. stellaris (r, p)

Hemiaulus haucki (r, p)

Rhizosolenia alata (r, p)

Silicoflagellate:

Dictyocha fibula (r, p)

Dinoflagellates:

Prorocentrum micans (a) Ceratium furca (r)

3. HYDROID-PHASE (Fig. 4)

By the end of the fourth week, hydroids invaded the panels in different degrees; being most conspicuous on plexiglass. Two species of hydroids were particularly abundant, viz: Obelia dichotoma (L.) forming creeping colonies about 3 cms. long, and another species (Hydroid II in fig. 2) which is tentatively referred to Eudenderium rameum (Pallac). The latter formed erect colonies, a few millimeters high on the edges of plexiglass panels which were more exposed to agitation by water.

The diatoms, along with bacteria, became conspicuous on most

netallic sheats.

A quantitative study of the fouling community at this stage is shown in the following table. Organisms enclosed in an area of 1 quare inch (6.25 cm^2) taken at random on a plexiglass panel 6" 15 cm) $\times 4$ " (10 cm) were counted under the microscope. The numbers below no doubt represent minimal quantities, since some of the organisms involved are lost through transportation of the panel into the laboratory.

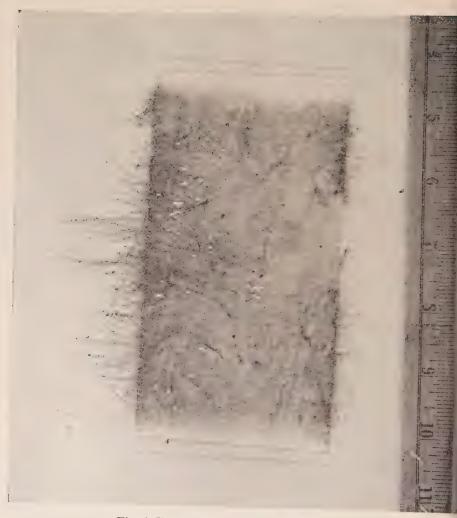


Fig. 4. Hydroid-phase on a plexiglass panel.

TABLE I

Populations on plexiglass panels after 4 weeks.

Organism									_		No./sq. inch (6.25 cm ²)
Bacteria			٠	٠		٠		۰			Infinity
Diatoms	٠					٠	٠				50,000 (Including 3800 individuals of <i>Cocconeis</i> alone).
Ciliates .			۰			۰		٠	۰	٠	360 (individuals)
Hydroids				٠		٠	۰	٠	٠	٠	40 (colonies)
Copepods											
Ectocarpus	S	sp.		٠	٠	•	٠	0	۰	۰	10

Although copepods and most ciliates are not sedentary organisms, their presence in the community is possibly attributed to the diatoms and bacteria upon which they graze.

Ectocarpus appears for the first time, following invasion of the

panels by the hydroids.

Some authors (e.g. Huvé 1953) do not distinguish the hydroids as a separate phase, but include it in the *Ectocarpus* phase. This may possibly be due to the fact that the periods between which panels have been examined by Huvé were too long (monthly intervals).

Ectocarpus, as will be seen, becomes dominant in the following

phase.

A list of diatoms from vinyl acetate, plexiglass and wooden substrata includes most of the species already encountered in the diatom-phase with the following additions:

Striatella unipunctata (a)
Licmophora abbreviata (a)
Rhabdonema mirificum (f)
Synedra tabulata (c)

Caloneis sp. (r)
Tropidoneis lepidoptera (r)
Nitzschia pacifica (r,p)
Amphora decussata (f)

4. ECTOCARPALES-PHASE

Between the sixth and eighth week following immersion, a phase dominated by *Ectocarpus granulosus* and *Myrionema sp.* was apparent on all panels, particularly on wood. Tufts of *Ectocarpus* reached 5 cms. long on the latter substratum; much less so on copper plates. This alga together with a *Polysiphonia* were also identified on the iron frames supporting the panels.

The Myrionema formed discs, 3-5 mm. in diameter from which

erect filaments, 5—8 mm. long, bearing sporangia, arose.

While these two *Ectocarpales* dominated this phase, other growths also existed, viz: bacteria, diatoms and hydroids. Among colonial



Fig. 5. Early stage of the Balanus-phase on wood.

diatoms, Schizonema ramosissima formed gelatinous tubes, 1.5 cm. long. However, the area covered by diatoms considerably diminished than during the diatom-phase.

Particularly on wood, a decapod, Emerita analoga together with

the amphipod Caprella were not infrequent.

In addition to the above organisms, a few Sabellid worms grew on wooden panels, particularly near the edges.

5. BALANUS-PHASE (fig. 5)

Balanus tintinnabulum californicus settled, in varying quantities, on the different panels after the seventh week of immersion. This barnacle invades the wooden panels as well, and settles more evenly on the more sheltered surfaces, but showed a more or less contageous distribution on exposed ones. It was not as abundant on plexiglass, glass or copper.

The largest individuals of *Balanus* seen on May 26, on the test panels, measured 6—8 mm. in diameter; the majority of the rest

measured 3-5 mm.

The quantity and, to a certain extent, the quality of the settling organisms may differ on both surfaces of one and the same panel as illustrated in the following table.

TABLE II

Frequenty of the chief animals and plants settling on two different surfaces of a wooden panel 14'' (35.5 cm) \times 10'' (25.5 cm) immersed for 8 weeks.

(The following symbols are also used for convenience:

++++ abundant, +++ common, ++ frequent, + rare, — absent)

Organism	Exposed surface	Protected surface
Barnacles	3 indiv./sq. inch.	Ca 1—1½ indiv./sq. inch.
Tube worms	+++	++
Nudibranchs	+++	+++
Hydroids	++++	++++
Bryozoa	+++	++
Bacteria	infinity	infinity
Diatoms	. ++	+++
Ectocarpus granulosus	++	+++
Myrionema sp.	++	++
Polysiphonia flaccidissima	++	_
Platythamnion sp.		+
Ceramium pacificum	_	+
Young encrusting algae		
(Lithothamnion?)	+	++
Acrosorium uncinatum		+

ELAVATION OF SUBSTRATUM

During this phase too, the substratum, especially on protected surfaces of wood, was raised through the accumulation of organic debris, sand particles and small colonies of *Bryozoa* and tube worms, all of which were cemented together. This biotope harboured a large number of diatoms and microfauna such as foraminifera (e.g. *Discorbis*), ciliates (*Vorticellids*), *Turbellaria*, together with small crustacea.

The barnacle-phase continued throughout June and until these observations came to an end. At such a stage, barnacles were particularly abundant on wood and glass panels, reaching a diameter of about 2 cm.

6. BRYOZOAN-PHASE

By the end of the twelfth week, colonies of a *Bryozoan*, resembling *Membranipora*, 1—2 cm. in diameter were seen on plexiglass, copper and wooden plates. They were most conspicuous towards the edges of these panels, which also sustained barnacles, hydroids and other growths. Again, careful examination revealed the presence of small bivalved mollusks.

Of the encrusting algae, *Lithothamnion* and *Melobesia* (?) -like discs were more conspicuous on plexiglass and glass panels.

Other algae, not previously noticed include *Colpomenia sinuosa* and kelp sporlings; these were particularly identified on wood. Though this early *Bryozoan* stage does not actually merit being called "phase", it is here included owing to its invariable occurrence on most of the panels.

A summary of the frequency of the main fouling organisms on 4 different substrata during this experiment in shown in table III.

DISCUSSION

Establishment Of Biotic Succession:

Thirty years ago, WILSON (1925) made observations on marine algal succession between January and May near the Scripps Institution at La Jolla. He used wooden blocks, denuded rock surfaces as well as glass plates suspended near the water surface from the Scripps Pier. Although his experiments suffered from sand scouring, he

TABLE III

Summary of the distribution of fouling organisms on different substrata immersed at a depth of 45 feet (ca 14 m) (roman numbers indicate the number of weeks following immersion, abundant; ++ frequent; + rare or infrequent; — absent).

Substratum:	Plexiglass				Glass					W		Copper				
Weeks:	I	II	IV>	(II)	I	II	IV	XII	I	II	IV	XII	I	II	IV	XII
ria	+++	++	++ (++	++	+	+	+	++	+	+	+	+	++	++	+
ms	+	+++	+++	++	+	++	+++	++	++	+++	++	++			++	+++
roids	_	+	+++	++		+	++	+++		++	++-	+ ++		+	+	++
arpales			+	++			_	++			++-	+ ++	_	_	+	++
asting algae		_		++				++		_		. +	_			+
worms	i —		+	++		_		+		_	- -	+ +	_		_	+
acles				+++		_		+			_	+++	_			+
zoa	_														_	+
usks	-	_		++	_	_		+	_		_	++		_	_	+

arrived at important conclusions regarding algae succession which could be summarized as follows:

Diatoms ——— Hydroids ——— Ectocarpus ——— (Ulva, Enteromorpha, Scytosiphon) ———— Pre-kelp-association and finally a kelp association.

COE & ALLEN (1937) summarized results of 9 years observation on the growth of sedentary organisms on experimental blocks and plates in the same region, yet they did not distinguish between seasonal progression and veritable succession as pointed out by SHEER (1945). The latter author made prolonged observations at Newport Harbour, California and arrived at two important conclusions, viz:

- 1. That the sedentary "communities" on the various experimental substrata were dominated respectively by: algae (bacteria and diatoms) Bryozoans, Ciona, Styela, and Mytilus.
- 2. That these communities represent stages in ecological succesion.

While the above mentioned experiments were made in the Pacific, Huvé (1953) made experiments on similar lines in the Mediterranean at Banyuls. His succession "Phases" could also be summarized as such:

Bacteria — Diatoms — Ectocarpaceae - Hydroids — Enteromorpha — Ulva. The *Ulva*-phase includes two subphases, *viz*:

a) An upper stratum dominated by Ulva and epiphytes, b) a

lower stratum dominated by Bryozoa, encrusting algae, ascidia,

hydroids and other sciaphilic forms.

My observations at Banyuls (unpublished) on algal colonization on floating cork used by fishermen in the summer of 1951, revealed the following succession which support, to a great extent, that of Huvé made over a much longer period: Bacteria — Diatoms — Ectocarpus — Hydroids — Enteromorpha — Ulva.

In England, HARRIS (1943) distinguishes three stages in succession, viz: a) Bacterial slime, b) Diatom flora, c) Higher animals.

It appears from the foregoing that the two universally recognized pioneer phases in the colonization of newly submerged substrata in the sea are undoubtedly the bacteria and the diatoms. As previously pointed out the bacterial phase had readily been overlooked by most earlier workers, probably as a result of its inconspicuous appearance, except on transparent substrata.

The above experiments have all been made at or near the surface and the succession phases are characterized by a green alga stage dominated by *Enteromorpha* or *Ulva*. GRAHAM & GAY (1945) in

Oakland, California also include such a stage in their results.

The absence of a green alga phase in my experiments, is most probably to be attributed to lack of sufficient light, since my test panels have been immersed in deeper water. The light intensity at such a deph was found to be 3—4% of that at the surface. On the other hand, a green algal phase dominated by *Enteromorpha* and *Ulva* was common, at the time, at the water surface on the pier supports and buoys in the neighbourhood.

Although these observations are of a relatively short duration, yet they support, to a great extent the conclusion arrived at by SHEER (p. 109), that the changes observed on the different substrata are similar and independent of the nature of the submerged surface.

Biotic succession and seasonal progression:

There is little doubt that on denuded surfaces or on newly submerged substrata in the sea, a certain order of succession of marine organisms dominated by various phases takes place. These dominant phases may not necessarily be recruited from the plants and animals found in abundance on the natural substrata in the neighbourhood of the experiment. SHEER (p. 117) stressed studying the breeding season of the organisms involved, length of free-swimming larval periods and their settling habits, beside the life span of the organisms themselves. He found little or no bryozoans on plates exposed for 4 weeks during winter, despite the fact that settling larvae of these organisms are present in the water during the same period. Also,

while the breeding seasons of most of the organisms involved in the sequence described by Sheer extend through most of the year, yet definite succession on his panels was distinguished.

This is also supported, to a certain extent, by the present experiment, where examples may be derived at least from the algae. Several species of short life-spans belonging to *Enteromorpha*, *Ulva*, *Scytosiphon* and *Ceramium*, found in abundance in reproductive

stages in the neighbourhood, failed to settle on the panels.

Whether colonization takes place at the surface or in deep water, the two pioneer phases are bacteria and diatoms. Subsequent phases may be modified according to locality and prevailing ecological conditions. Variations as to the identity of such subsequent phases is a matter which probably also depends much upon the time interval between which the test panels are examined, as well as upon the growth rate of the organisms involved.

Such ecological succession may lead to a climax and the climax in Californian water seems to be the *Mytilus* (cf. also SHEER, 1945). This organism was noticed on substrata supporting an advanced fouling community, in the region of La Jolla, e.g. buoys and pier supports at the surface; old anchors, ship remains etc, at the bottom.

Among the general characteristics of the succession stages in marine fouling communities is the decrease with time in the potential area colonized by the algae as suggested by Huvé(l.c.); in other words, the ratio of surface colonized by algae to that colonized by animals is greater than 1 at the start but considerably decreases later on.

Interrelations of the successive phases:

Biotic succession of the different phases of the fouling community is determined by a set of factors working together, which may be analysed as follows:

1. Mechanical support: This is afforded by the pioneer stages (bacteria and diatoms) for subsequent organisms through mucous secretions which may capture organisms or spores of the latter. The rôle of bacteria has been emphasized particularly by ZOBELL & ALLEN.

Mechanical support may take another form as the community advances in growth. This is manifested by increasing the effective surface for attachment during competition for space. Thus barnacles may settle on bryozoans; algae and hydroids may settle on tube worms and barnacles, as well as on the elevated substratum afforded by calcareous secretions.

2. Food relations: The relation between the different populations of the fouling community depends largely on food require-

ments. Once bacteria and diatoms settle, protozoa, including ciliates, and *Turbellaria* follow. Even nonsedentary forms like copepods, isopods and amphipods are attracted to panels sustaining such early growths.

Copepods and ciliates have been observed te devour large numbers of diatoms. Small crabs which also live in this biotope prey upon Caprella and small crustaceans; nudibranchs upon hydroids.

Animals feeding on detritus such as amoeba, flagellates, as well as filter-feeding animals, such as hydroids and barnacles, find a niché

in this biotope.

It has also been observed that the organisms forming the different phases in the fouling community persist during the subsequent phases, they are never altogether eliminated from the system. The rate at which food is produced and consumed, together with the length of generations will determine the population balance in the community.

3. Che mical changes: Certain metabolic products e.g., humin, lipids, amino acids, carbohydrates and vitamins, produced in the medium as a result of bacterial action, excretion or lyasis may determine the nature of organisms to settle next. Some such metabolites may either be favourable for certain organisms or detrimental for others.

On the other hand, changes in the pH in the microclimate of the substratum due to the growth of certain populations may have an influence in determining the biologic sequence observed. Observations in cultures show that certain peridinians disappear, while others, accompanied by ciliates, increase in numbers, with the decrease in the pH of the medium (Aleem, 1952).

4. Physical changes in the microclimate: Physionomic changes in the fouling community during its growth bring about prominent changes in the microclimate itself. There are thus areas created in the same substratum which receive less light than others. Certain tunicates, bryozoans, boring organisms as well as Lithothamnion and Peyssonnelia find good nichés in dim light and readily colonize such areas. Obligate parasites or epiphytes may consequently follow their characteristic hosts.

SUMMARY

An experiment was made in which artificial substrata immersed during 12 weeks at a depth of 45 feet (ca 14 m) below mean sea level, were periodically examined in situ by means of aqualung diving, as well as in the laboratory, in order to study succession of marine fouling organisms. Results may be summarized as follows:

- 1. A biological sequence was manifested by the following phases in succession: bacteria, diatoms, hydroids, ectocarpales, barnacles and bryozoa. These populations once they settle, are not subsequently eliminated from the system, though their abundance may vary considerably in magnitude.
- 2. This succession is essentially similar to that produced at the surface with the elimination of a green alga-phase which may be due to insufficient light.
- 3. The successive phases are independent of the nature of substratum. The rôle played by the latter may result in lagging in time of settling of these organisms, retarding their growth or affecting their quantity.
- 4. Biotic succession seems also independent of seasonal variations of the organisms concerned.
 Generally speaking, the panels nearer to the bottom support less growth than those higher up, which may be due to the scouring effect of the sand at the bottom. Besides, the amount of growth
- may sensibly differ between the two surfaces of the same panel.

 5. The experimental panels may be arranged according to their suitability for growths in a descending order as follows: Wood,

plexiglass, vinyl acetate, glass, brass, zinc, stained steel and copper.

- 6. Interrelations of the successive phases are discussed. Stress is made upon the food relations in the fouling community.
- 7. The fouling community is considered as a growing mechanism, manifested by successive phases which may ultimately lead to a "climax". The factors affecting this mechanism are complex and involve both physical and chemical changes in the substratum, as well as complex food relations among the surviving generations. Foreign animals and plants such as crabs, fish, encrusting algae etc, may find suitable nichés in this biotope and consequently add to the complexity of the system.

This work was done at the Scripps Institution of Oceanography, La Jolla, California, while the writer was a holder of a Fulbright grant. Acknowledgment is made to the staff of this institution, particularly to admiral Charles Wheelock and Dr. Francis Haxo. Special thanks are due to Professor Martin Johnson and Professor Claude Zobell for discussions, to Mr. Conny Limbau for help in designing the experimental cage, to Dr Robert Menzies for help in identifying the crustaceans and to Mr. Jim Gordan my co-diver in under-water operations.

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Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere

by

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The ponds, which were formed about 50 years ago by damming, are on Claife Heights, a low range of hills rising to 200 m. above sea level to the west of Windermere. Collecting was done chiefly in two ponds, Scale Tarn and Hodson Tarn, which are in neighbouring valleys about half a mile apart. In a third pond, Wise Een Tarn which has been studied earlier (SMYLY 1952), the open water was sampled regularly but weed-beds infrequently. The ponds lie on boulder clay or thin peat overlying Bannisdale slate. They are similar chemically (pH 6.8, Ca + 5.0 p.p.m.) and have a mean depth of about 1 m and a maximum depth, at the dams, of about 15 m. Scale Tarn (6,100 m²) and Hodson Tarn (4,700 m²) are similar in size and smaller than Wise Een Tarn (44,500 m²). Scale Tarn and Wise Een Tarn are in relatively open positions but Hodson Tarn lies in a hollow sheltered on three sides by wooded slopes. Only small seasonal variations in water level were noted. Ice covered the ponds for at least a few weeks in winter and persisted longer on Hodson Tarn than on the other two ponds.

Carex rostrata was common in shallow water: in Hodson Tarn it was confined to a single bed choked with rotting stems to knee depth through which bubbles of gas smelling of hydrogen sulphide rose; in Scale Tarn it formed an almost continuous fringe relatively free of detritus. Beyond the Carex zone, there was a small amount of Potamogeton natans in both ponds. In deep water the bottom supported Myriophyllum sp. in Hodson Tarn and Nitella translucens in

Scale Tarn.

When the present observations began in April 1951, the ponds had

been undisturbed since December, 1948, when both ponds were drained to remove fish. Myriophyllum was then common in Hodson Tarn and Nitella almost filled the whole central region of Scale Tarn. During the period of the present observations, April 1951 to December 1953, Hodson Tarn remained undisturbed and Myriophyllum became increasingly luxuriant in the middle of this pond but Scale Tarn was drained and refilled in July and October 1951. Both the Nitella and Potamogeton were destroyed by these drainings leaving the middle of this pond virtually free of all weed during the investigation. Collecting was done in weed-beds and in open water but the bottom mud in deep water was not sampled. The marginal weeds in Scale Tarn were sampled at four positions which were chosen as typical of different parts of the pond but in Hodson Tarn only the single weed-bed was sampled. The ponds were visited fortnightly in 1951 and 1952 and once a month in 1953, except from July to December 1951 when no regular collecting was done in Scale Tarn because this tarn was drained twice in this period, and from April to July 1951 when Hodson Tarn was not visited.

METHODS

The middle of the ponds was sampled with a tow-net (60 meshes/in.). In Wise Een Tarn it was towed behind a boat for the same length of time on each visit and care was taken to sample only deep water free of weeds; at the other two ponds where there were no boats, the net was cast from the dam on a line 14 m. long, five casts being made at each visit. Collecting was usually done between 10 a.m. and noon but, because diurnal migrations have been found even in shallow ponds (VAAS & SACHLAN 1953), on one occasion in Wise Een Tarn collections were made one hour before and two hours after sunset; no difference in relative abundance of species was found. Marginal weeds were sampled by trap, pond-net and trays on the bottom. The trap was a metal tube, 52 cm long and 8.5 cm in diameter, which sampled a vertical column of water. The lower rim was sharpened to form a cutting edge and the upper, blunt rim was fitted with a lid. Samples were taken by lowering the tube, with both ends open, vertically into the water until it touched the bottom when a further downward thrust closed the bottom with a plug of bottom material. Usually a plug 2" deep was sufficient to retain the water column when, with the lid in place, the tube was raised, but the exact size of plug was unimportant, as virtually all Entomostraca were removed if a portion of the water column was first strained off, and the surface mud then rinsed off with the remainder of the water. The variation in numbers of

most species in replicate samples fitted a Poisson distribution and, although such variation was occasionally markedly non-random, estimates of abundance were made on only three tube samples at each sampling station because more time than that needed for counting this number of samples was not justified by the fractional increase in accuracy gained in doing so. In comparison with the Macan grab (1949) the tube caused less disturbance at the moment of sampling and less damage over a period of time; it also caught more scarce species, especially species living on or near the bottom. More scarce species were also caught in the tube than in a pond-net. However the tube, as described, can only be used at wading depth, it takes a firm plug only on clay, and may fail to catch Entomostraca at the surface. The pond net was conventional with 60 meshes per inch. The tray was a metal framework which held nine open-mouthed bottles (diameter 8.5 cm and 8 cm deep). The trays were left on the bottom for twenty-four hours before lids were put on in situ.

Counting was done in a trough under low magnification. Any detritus left after rinsing the sample through bolting silk (60 meshes/in.) was spread out as thinly as possible on the bottom of the trough. Attempts to separate the animals from the detritus by adding calcium chloride or magnesium sulphate were only partly successful as 20 %— 40 ° of the animals failed to rise to the surface. Total counts were made on all tube and tray samples and on those tow-net samples with less than about 300 animals, but in large tow-net samples with more than about 300 animals, counts were made on 5 ml fractions taken with a Stempl pipette. Identification was carried out with the keys of Scourfield and Harding (1941), Gurney (1931—33) and Klie (1928) for Cladocera, Copepoda and Ostracoda respectively.

Copepoda and Ostracoda respectively.

DISTRIBUTION OF SPECIES

Table 1, which summarises data from all collecting methods, shows that more species were found among weeds than in open water. Although relatively few species were found in open water, visual comparison of samples from open water and weeds indicated a quantitative abundance in open water similar to that in the weeds. Species caught abundantly in open water were Diaptomus gracitis, Daphnia longispina, Ceriodaphnia pulchella, Bosmina longirostris and Polyphemus pediculus and of these five species only Daphnia longispina was rare in weed-beds. Tow-net collections in the middle of Scale Tarn (which was free of weeds) were similar to those in Wise Een Tarn (where weeds could be avoided) except for Cyclops leukarti which was quite numerous in Wise Een Tarn but scarce in Scale Tarn. In

 $\label{eq:table_table} TABLE \ \ \textbf{1}$ Distribution of Entomostraca in two moorland ponds.

Order	Species	Mid- Tarn	Carex		Nitella or Myriophyllun	Bott Detritus	
Conenada	Cyclops viridis	+	+++	++	++		
Борероци	Cyclops albidus (Jurine)	+	+++	++	++		
	Cyclops agilis s.s. (Koch, Sars)	+	+++	++	++		
	Canthocamptus staphylinus (Jurine)		+++			++	
	Diaptomus gracilis Sars	+++	+++	++			
	Cyclops fuscus Jurine		+-+-	++			
	Cyclops affinis (Sars)		++			+	
	Cyclops fimbriatus (Fischer)		++			+	
	Cyclops macruroides s.s. Lilljeborg		++	++	+		
	Cyclops macruroides denticulatus Graeter		++	++	+		
	Cyclops bicolor (Sars)		+				
	Cyclops bisetosus (Rehberg)						
	Canthocamptus crassus Sars		+			+	
	Cyclops leukarti (Claus)	++	+	-1-			
	Cyclops phaleratus (Koch		+			+	
			+				
	Cyclops nanus (Sars)						
Cladocera	Chydorus sphaericus Baird	+	+++	++	+++		
	Chydorus piger Sars		++				
	Simocephalus exspinosus (Koch)		+++				
	Eurycercus lamellatus (O.F. Müller)		++	÷÷	+++		
	Ceriodaphnia pulchella Sars	+++	+++	++	+		
	Alona rectangula Sars		++	+			
	Alona alfinis (Leydig)		++	+			
	Ilyocryptus sordidus (Liéven)		+				
	Pleuroxus trigonellus (O. F. Müller)		++	+			
	Sida crystallina (O. F. Müller)		++	+++			++
	Graptolebris testudinaria (Fischer)		+	- 1			
	Pleuroxus laevis Sars		+	+			
	Alonella exigua (Lilljeborg)		+	+++			
	Daphnia longispina (O. F. Müller)	+++	+				
	Drepanothrix dentata (Euren)		,			+++	
	Polyphemus pediculus L.	++	+	+++	+		
	Diaphanosoma brachyurum (Liéven)	++	+	'++	++		
	Peracantha truncata (O. F. Müller)		++	+++	++		
	Bosmina longirostris (O. F. Müller)	++					
	Bosmina obtusirostris Sars		+	+	73		
	Chydorus globosus Baird		ela.	+	+		
	Alonella nana (Baird)		+	++			
	Streblocerus serricaudatus (Fischer)		+				
	Acroperus harpae Baird		+				
	Monospilus dispar Sars		+				
Ostracoda	Candona candida (O. F. Müller)		+			++	
	Cypira exsculpta (Fischer)		+			+++	
	Cyclocypris ovum (Jurine)		+			+	
	Cypricercus obliquus (Brady)		+			+	
	Eucypris clavata (Baird)		+			+	
	Cypridopsis vidua (O. F. Müller)		+			+	

tow-net collections in Hodson Tarn (where Myriophytlum could not be avoided by the net) Diaptomus gracilis was abundant, Daphnia longispina and Ceriodaphnia pulchella were scarce, Diaphanosoma brachyurum was numerous, and Cyclops leukarti not found. In addition several weed-dwelling species, especially Chydorus sphaericus, were found. Scarcity of Daphnia longispina in Hodson Tarn is clearly associated with the presence of Myriophyllum in the deep water of this pond, for both in Scale Tarn and in Wise Een Tarn (SMYLY 1952) it was always scarce or absent wherever weeds were sampled, and there are several references in the literature to scarcity of this species in weeds. The distribution of Ceriodaphnia pulchella and Diaphanosoma brachyurum in these ponds is difficult to account for. In Scale Tarn, Ceriodaphnia pulchella was abundant both in weeds and in open water, yet in Hodson Tarn it was scarce; Diaphanosoma brachyurum is known to be a pelagic species which sometimes occurs in weeds (BERG 1929) yet in these ponds it was rare both in the marginal weeds and in open water, and was found chiefly in the weedy middle part of Hodson Tarn and also in the middle of Wise Een Tarn but only among Nitella. In his survey of a neighbouring pond, Three Dubs Tarn, MACAN (1949), quoting some records of Dr C. H. MORTIMER, notes that D. brachyurum formed less than 10% of the open water Crustacea in July 1936 when there was little weed in the middle of this pond but in June 1947, when Nitella "formed a fairly uninterrupted sward" it was the commonest species in the plankton. It seems possible that these two species are in competition, a weedy middle region favouring D. brachvurum and open water favouring C. pulchella.

The distribution of species in marginal weeds was studied by comparing the mean numbers of each species caught by the tube at each collecting station in Scale Tarn. Forty-seven species were caught in weeds of which sixteen were abundant (over 30/litre) twenty-two were numerous (10—30/litre) and nine rare (never over 10/litre). It is difficult to generalise about distribution, which varies from random to bunched in all species; some species tend to be distributed at random and others to be bunched more often than others whereas many species are distributed at random as often as not. Cyclops viridis and C. albidus, in particular, were randomly distributed most often and non-random distribution was more common among Cladocera than Copepoda. A good example of such a cladoceran is Polyphemus pediculus, swarms of which have been seen on several occasions in the fringes of and in open spaces between Potamogeton leaves. From the pattern of local distribution found at different times and in different parts of the same pond at one particular time, it was deduced that whereas several species occur in almost any kind of weed, others are more commonly associated with some particular kind of weed or type of bottom. Thus, *Sida crystallina* is common beneath floating leaves of *Potamogeton* (see Table 2) where up to 20 *Sida* may be found if

TABLE 2

Entomostraca found among floating leaves of Potamogeton natans

	(a)	coll	ected	by (cutt	ing off le	(b)	(b) collected with pond-net						
Species of Eulomostraca	,	Wise	Een	Tar	n	Hodson Tarn	Wray- mires Tarn	Hodson Tarn	Hodson Tarn Wise Een Tarn					
	24 July	31 July	24 Aug.	18 Sept.	9 Oct.	18 Sept.	7 Aug.	18 Aug.	22 Aug.	24 Aug.	28 Aug.	18 Sept.	9 Oct.	23 Oct.
Sida crystallina	58	136	46	IOI	96	81	222	133	107	198	61	66	114	100
Peracantha truncata	I	23	107	I	13	1	I	37	48	89	022	96	65	IOI
Alone la exigua	10	47	170	0	0	I	199	0	0	55	0	0	0	I
Polyphemus pediculus	0	5	I	0	0	1	0	5	12	0	12	146	0	I
Other species	7	13	00	I	4	2	0	9	15	2	0	3	5	3

leaves are lifted and cut off quickly at the base but it was never found in the trays on the bottom and was always scarce in tube and pondnet samples in all weeds other than Potamogeton, except once when at the time of its maximum abundance it occurred abundantly in an adjacent Carex bed, perhaps because of over-crowding in the Potamogeton. Wesenberg-Lund (1905) Langhans (1911) and Berg (1929) also comment on association of Sida with Potamogeton. In Nitella, Eurycercus lamellatus, Chydorus sphaericus and Peracantha truncata were particularly abundant and Simocephalus exspinosus was often numerous in Carex. With one exception, those cladoceran species, which were abundant in Scale Tarn in either Nitella or Potamogeton in 1951, were scarce in the absence of these weeds in 1952. The exception, Chydorus sphaericus, in spite of being scarce in Carex (only 10/litre compared with 1000/litre in Nitella growing alongside) when Nitella was present, was as abundant in Carex in 1952 as it had been in Nitella in 1951. In a few instances, local distribution was associated with the character of the bottom. Ilvocryptus sordidus and Candona candida, two bottom-living species, were found more abundant on soft mud than on gravel or clay. In the River Susaa, Denmark, Ilvocryptus sordidus was most abundant on soft mud (Jonasson 1948). Where detritus lay on the bottom, Drepanothrix dentata and Cypria exsculpta were abundant. The former species is known to occur locally in woodland pools (HERR 1913, GURNEY 1914, BERG 1929).

The distribution of species at particular stations in the ponds was found by comparing the results of replicate tube samples in conjunction with tray and pond-net collections. Nearly all species showed

large variations in number on a few occasions and a few species did so on many occasions. Stems of Carex, the only common water weed in Scale Tarn after it had been drained, were occasionally centres of local aggregations but as a rule little difference was found between those tube samples taken directly over and those taken between Carex stems. Cyclops spp., in particular C. viridis and C. albidus showed less variation than most Cladocera. χ^2 analysis of the distribution of Entomostraca in open-mouthed bottles held in trays on the bottom showed that most species were distributed at random over an area covered by a single tray (0.09 m²) but bunched over larger areas and when numbers were large. Comparison of concurrent tray and tube samples shows that many species are taken in equal abundance by both methods. The open mouthed bottles, which had the same diameter but were only 1/6 as long as the tube, could be regarded as equivalent in sampling volume to the lower 1/6 of the tube. As laboratory observations showed that the bottles exerted little or no trapping effect on any swimming species, equal abundance of these species in both open bottles and the tube means that most such species were within about 10 cm. of the bottom in daylight. Species which live mostly at the surface e.g. Sida crystallina or on the bottom e.g. Ilyocryptus sordidus were always scarce in the open-mouthed bottles. On the other hand, two copepods, Cyclops agilis and C. macruroides and one cladecoran Simocephalus exspinosus were found more abundantly in the bottles than in the tube; in culture vessels all these three species were more often seen clinging to the vertical sides than swimming. In concurrent tube and sweep-net samples, free-swimming forms were caught only slightly more frequently but bottom-crawlers were taken two to three times as often by the tube as by the pond-net. Only Cyclops fuscus, which has a habit of hanging from the surface film, was taken more often in the pond-net than in the tube.

As the ecology of species which have close taxonomic relationships is of some interest, the relative abundance in Scale Tarn and Hodson Tarn of two Eucyclops species (and a variety of one of them) is shown in Table 3. It will be seen that Eucyclops macruroides s.s. and Eucyclops macruroides denticulatus Greater were relatively abundant in Hodson Tarn but scarce in Scale Tarn except for June and August 1951, and this suggests that they have more in common ecologically than either has with Eucyclops agilis s.s., which was abundant in Scale Tarn on all occasions but scarce in Hodson Tarn except for a slight rise in numbers in the spring of 1952.

TABLE 3

Totals of (a) Fucyclops agilis 8.8. (Sar	s), (b) Eucyclops macruroides s.s. Lilljeborg and
(c) Eucyclops macruroides denticulatus	Graeter in Scale Tarn and Hodson Tarn.

				JAN.	FEB.	MAR.	APR.	MAY	JON.	JUL.	AUG.	SEPT.	OCT.	NOV.	DEC.
		5	a	_			_		37 50	_	31 25	_	_	_	33
	1951	1	b c					-	24	_	21				0
ĺ		(a	_	_	20	44	72	67	69	_		46	-	29
SCALE	1952	- }	a b	-	_	I	0	0	I	7	_	_	0		2
TARN		(С	_		0	0	0	0	I	_	_	0		С
		(a		69	_		60	35	67		24	58	56	54
	1953	- }	a b c	_	69 0			0	0	0		2	2	4	6
•	L	(С	_	0	_	and the second	0	0	I		0	0	I	0
		(а	-	_	_	_		_	0	0	3	4	0	2
1	1951	3	b c	_	_		_	-		5	31	29	23	47	41
		(С	_		_		_	_	0	5	2	2	II	0
		(а	_		II	9	17	IO	3	2	0	5	0	
HODSON	1952	- {	b	_	_	53	44	31	. 4	6	16	17	7	5	
TARN		(С			6	15	II	26	26	35	24	15	43	_
		(a	3	0	I	0	3	_	6	_	0	3	2	2
	1953	3	Ъ	9	14	38	15	58	_	16	_	9	7	20	29
		(С	ΙI	12	24	ΙΙ	ΙI	-	13	_	19	36	80	27

SEASONAL ABUNDANCE

Seasonal changes in percentage composition of midtarn Entomostraca are shown in Fig. 1. Diaptomus gracilis forms the greater part of the catch in winter together with some weed species, especially Chydorus sphaericus, where the net has unavoidably passed through some weed. Between spring and autumn, varying proportions of Daphnia longispina and Ceriodaphnia pulchella, in particular, and also Diaphanosome brachyurum, Polyphemus pediculus and Bosmina longirostris, are present. A quantitative difference between Wise Een Tarn and Scale Tarn on the one hand and Hodson Tarn on the other (not shown in Fig. 1 where only percentages are given) was observed visually; in early March, Diaptomus gracilis is abundant in the townet (100-200 in 5 hauls) in Wise Een Tarn and Scale Tarn whereas in Hodson Tarn it is scarce (less than 10 in 5 hauls) at this time and only becomes abundant by mid-May. This difference is probably related to the later melting of winter-ice in Hodson Tarn which, because of its sheltered position, receives less sun and wind than either of the other two tarns. It should be mentioned also that Ceriodaphnia pulchella is at times very abundant in Scale Tarn but this is not apparent in the figure because maxima of this species coincide with even greater maxima of either *Diaptomus gracilis* or *Daphnia longispina*.

No essential differences between the different years of study are apparent in Fig. 1, except in Hodson Tarn where there is a noticeable increase, especially in 1953, in the percentage of weed species in the middle of the pond and a concurrent decrease in the percentage of planktonic species, a change thought to be associated with growth of

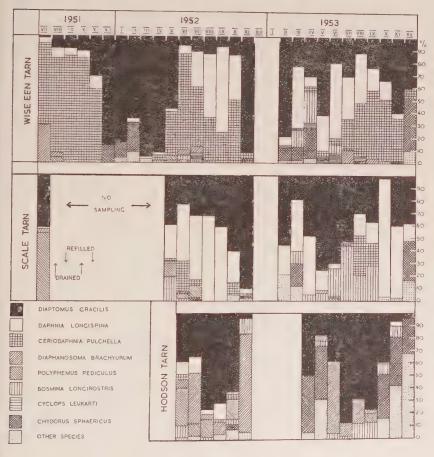
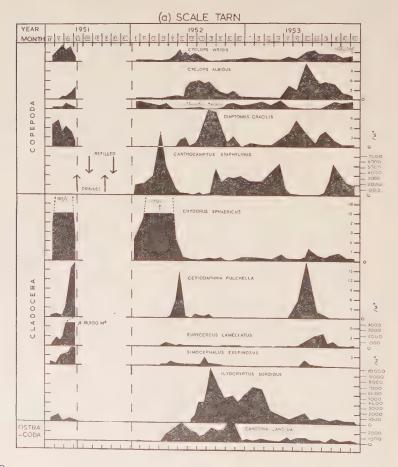


Fig. 1.

Seasonal changes in percentage of common Entomostraca caught by tow-net in open water. Percentages were calculated from at least 100 specimens and usually more than 250. There are no entries for December 1952 and January 1953 in any of the tarns and for February and March 1953 in Hodson Tarn because in these months less than 100 Entomostraca were caught.

Myriophyllum. Although in Scale Tarn only one collection was made before the pond was drained, it can be assumed from the abundance of Diaptomus, Daphnia and Ceriodaphnia in the 1952 and 1953 townet hauls that the draining of the pond had a negligible effect on the open water Entomostraca of this pond.

Fig. 2 shows seasonal changes in abundance of the common species caught in marginal weeds. Some species are seen to be common mostly in the cold months of the year, others in the warm; among the former were Canthocamptus staphylinus, Cyclops agilis and C. macruroides, and among the latter Diaptomus gracilis, Ceriodaphnia pulchella, Cyclops viridis and C. albidus, and also several Cladocera, Eurycercus lamellatus, Peracantha truncata, Simocephalus exspinosus, Sida crystallina and Pleuroxus trigonellus, species which were abundant before Scale Tarn was drained but scarce in 1952 and 1953. One species, Chydorus sphaericus, was abundant in spring and numerous



in winter but scarce at other seasons. Few species were ever completely absent in any month and among the Copepoda only two species, Canthocamptus staphylinus which was found encysted in the bottom mud in summer and Cyclops bicolor which encysted as stage III and IV copepodids in winter, were shown to be absent from the water at any one season, whereas most Cladocera passed the winter as resting-eggs but in several species a few parthenogenetic females survived the winter and adult females of one species, Chydorus sphaericus were found abundantly under ice thick enough to walk on.

In Hodson Tarn little difference in the seasonal periodicity of weed-dwelling species was apparent in different years but this was not so in Scale Tarn. Scarcity in 1952 and 1953 of weed-dwelling Cladocera which were abundant in preliminary collections in 1951 has been noted already and is almost certainly associated with the draining of the pond. When the pond was empty, a few small puddles remained and in these several species, chiefly copepods, were found. The fluctuations in numbers of three species could not be explained: Chydorus sphaericus, though abundant in the spring of 1951 and 1952, was scarce at this season in 1953. Ilyocryptus sordidus, first noted in June 1952, was abundant until January 1953 and then be-

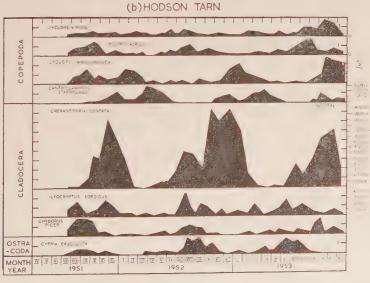


Fig. 2.

Seasonal changes in abundance of common Entomostraca caught by tube (mean of three samples) in weed-beds. Numerical values on the vertical sacle are given in number per litre (no./1). Because many Entomostraca live neither wholly on nor off the bottom, counts are also expressed as numbers per square metre (no/ m^2) by multiplying number per litre by 175.

came scarce; and Candona candida, a well-known winter form (ALM 1915, BERG 1938), was numerous from May to September 1952 but thereafter scarce. Scarcity of this species in winter may possibly be due to migration into deeper water which BERG (1938) found took place in Esrom Lake. It is well-known that Chydorus sphaericus varies greatly in seasonal abundance (BIRGE 1897).

Quantitative comparison of Scale Tarn and Hodson Tarn.

Scale Tarn has a greater number of abundant species than Hodson Tarn. In the middle of each pond a similar number of common species was found but on many occasions population numbers were much larger in Scale Tarn than in Hodson Tarn. In the marginal weeds, fourteen abundant species were found in Scale Tarn compared with only five such species in Hodson Tarn. Because many species, Cladocera in particular, which were abundant in the preliminary collections in 1951 were scarce in Scale Tarn in 1952 and 1953, the quantitative abundance of only a few species (Table 4) can be compared. It can be seen that most species, except detritus-dwellers, were considerably more abundant in Scale Tarn than in Hodson Tarn. One Cladoceran, Eurycercus lamellatus, which Dr. W. E. FROST tells me is the only cladoceran eaten extensively by fish in these ponds, attained a maximum of 19,800 m² in July 1951 in Scale Tarn but was much less numerous in 1952 and 1953 and was not found in Hodson Tarn in any of the three years. Since the investigation was completed, this species has appeared in Hodson Tarn in the summer of 1954 but only in the *Potamogeton* zone.

SUMMARY

- 1. Distribution and seasonal abundance of Entomostraca in moorland ponds near Windermere have been studied from April 1951 to December 1953.
- 2. The middle of the ponds was sampled by tow-net (60 meshes/in.); marginal weeds were sampled with (i) a metal tube which takes a vertical column of water from surface to bottom, (ii) a pond-net and (iii) metal trays which hold open-mouthed bottles.
- 3. More species were found among water plants than in open water and, of the latter, the only abundant species rare in weed-beds was *Daphnia longispina*.
- 4. Local distribution was common and in some instances was related to particular plants or the character of the bottom. In replicate

samples, many species were often distributed at random but some tendency to bunch was found in all species.

5. Seasonal periodicity of most common species was found; both warm and cold-water forms were present.

6. An increase of weed species and a decrease of planktonic species, associated with development of *Myriophyllum* in the middle of Hodson Tarn, was observed during the period of study, but in Scale Tarn long term trends were obscured by the drainings of the

pond in 1951.

TABLE 4
ean and maximum numbers of Entomostraca in tube collections in marginal weeds.

			S	SCALE TARN	TA	N N			НО	DSO	HODSON TARN	ARI	7
в	(a) Swimming species numbers per litre	April-June Max. Mean	April-June Max. Mean		1952 1953 1950 1952 1953. Jan-Dec. Jan-Dec. Jan-Dec. Jan-Dec. Jan-Dec. Jan-Dec. Jan-Dec. Jan-Max. Mean Max. Mean Mean Max. Mean Mean Max. Mean Mean Mean Max. Mean Mean Mean Mean Mean Mean Mean Mean	Jan- Max.	1953 Jan-Dec. Aax. Mean	July Max.	July-Dec. Max. Mean	Jan- Max.	Jan-Dec. Max. Mean	Jar	Jan-Dec. Max. Mear
Copepoda	Diaptomus gracilis	56	12	29	4	22	m	15	1/2	8	н	н	н
	Cyclops viridis	9	4	9	63	V	H	7	н	4	7	8	7
	Cyclops albidus	00	63	24	4	12	4	M	3	30	н	9	73
	Cyclops fuscus	0	0	0.3	0.3	0.3	0.3	77	н	I	0.3	H	0.3
	Cyclops agilis	2	X	3	Н	3/1	H	0	0	0	0	0	0
Cladocera	Chydorus sphaericus	87	42	203	14	6	7	Н	I.0	7	0.3	н	н
	Ceriodaphnia pulchella	0	0	32	33	57	9	0	0	0	0	0	0
Н	Bottom and detritus living species numbers per square metre												
Copepoda	Canthocamptus staphylinus	12,000	2,200	12,000 2,200 14,525 2,100 8,575 2,450 4,010	2,100	8,575	2,450	4,010		3,150	415 3,150 700 2,450	,450	875
Cladocera	Chydorus piger	0	0	OI	н	63	Н	H	0.7	2	H	7	73
	Drepanothrix dentata	0	0	0		4,025	1,050	1,575	175 1	226,93	0 4,025 1,050 1,575 175 16,975 7,000 4,550 2,100	,550	2,100
	Eurycereus lamellatus	19,800	5,075	19,800 5,075 612	o 476 o	1,487	476	0	0	0	0	0	0
	Hyocryptus sordidus	0	0	0 30,450 4,375 17,675 1,400 2,800 1,350 3,675 2,100 2,800 1,225	4,375	17,675	1,400	2,800	1,350	3,675	2,100 2	3800	1,225
Ostracoda	Candona candida	0	0	0 13,125 1,925 2,450 525	1,925	2,450	525	525		1,400	175 1,400 525 175	175	175

7. Abundant species were more numerous and occurred in greater abundance in Scale Tarn than in Hodson Tarn.

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The longitudinal succession of water characteristics in the White Nile

by

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INTRODUCTION

Successive modifications of water characteristics, both physical and chemical, can be expected to occur during the seaward flow of water in a river. Although knowledge of such changes is essential for many aspects of river biology, very few detailed studies are available, particularly for the large tropical rivers. This paper is concerned with changes in water properties along an important branch of the Nile system, the White Nile, for which little previous work exists (Beam, 1906, 1908; Lucas, 1908; Hurst, 1925, pp. 67—73; Tottenham, 1926; Brook & Rzóska, 1954; Beauchamp, 1956). The White Nile branch is one of the two main divisions of the upper Nile and extends for 2530 km between Lake Victoria and Khartoum, where it unites with the other division, the Blue Nile. The combined waters then flow, as the Main Nile, for a further 3080 km to the Mediterranean. This Main Nile region is not described here, and later references to the 'river' apply only to the White Nile sector.

This study was undertaken mainly as a background to a survey of river biology being made by the Hydrobiological Research Unit of the University College (now University) of Khartoum. Biological implications are therefore emphasized, and particular attention is paid to plant nutrients. Many features are also of considerable intrinsic interest, as would be expected for a river flowing northwards through several climatic and altitudinal zones, receiving the contributions of diverse drainage basins, and traversing a major African

swamp system.

The data are chiefly based upon samples collected along the river

in two seasons, May – June 1954 and December – January 1954-5. Results of the longitudinal survey are given here in graphical form, and interpreted in relation to the two chief modifying influences, tributary contributions and riverain swamps. In the lowest part of the river, which is a reservoir region, further modifications arise from the activities of seasonal plankton populations (cf. Brook & Rzóska, 1954; Rzóska, Brook & Prowse, 1955) which will be described in a

Separate paper.

Detailed information on the geography and hydrology of the White Nile is readily available (Hurst & Phillips, 1938; Newhouse, 1939; Hurst, 1950, 1952). The river flows out from Lake Victoria, and passes through parts of two lakes, Kioga and Albert, before falling steeply to the Sudan plain (profile in Hurst & Phillips, 1938, plate 5). Here it soon enters a large swamp (the 'Sudd') extending about 500 km along the river, in which about half of its water is lost. Near the end of the individual river at Khartoum the water is seasonally stored by the Gebel Aulia dam, whose influence extends a considerable distance upstream (Brook & Rzóska, 1954). The principal tributary drainage is from Lake Albert, several torrents near the Sudan border, and the River Sobat (fig. 1); the two latter contributions show large seasonal variations.

The river water is moderately rich in dissolved salts and has a marked alkaline reaction (pH usually 7.5 to 8.5) except when locally modified by swamp drainage. Like many other African waters (but unlike those in many other regions) calcium ions make up only a small part of the total cations present, sodium and potassium being predominant. As is usual in freshwaters, bicarbonate is the principal anion.

METHODS

Most of the work was carried out between 26 May – 25 June 1954 and 11 December – 8 January 1954-5, during two cruises of the research launch 'Malakal' between Khartoum and Juba in the south Sudan. Chemical analyses were performed within a few hours of sampling, pH being determined colorimetrically immediately after collection. During 26-28 May 1954 further samples were taken between Lake Victoria and Juba and analysed after a delay of 1 to 4 days (pH excepted). Some analyses were made during a previous cruise, in December 1953, along the river stretch 1000 km southwards from Khartoum.

Analyses carried out (on filtered samples) by standard methods described by the AMERICAN PUBLIC HEALTH ASSOCIATION (1946) and TAYLOR (1949) included ammonia (direct Nesslerization), nitrate

(phenol disulphonic acid, including decolorization with aluminium sulphate), silicon (ammonium molybdate), phosphate (ATKINS' modification of DENIGES' method), and chloride (titration with silver nitrate). Sulphate was estimated turbidimetrically after precipitation with barium chloride (WERESCHTSCHAGIN, 1931) and calcium by the versenate titration method (Heron & Mackereth, 1955). Total iron was measured colorimetrically using ammonium thiocyanate after a preliminary oxidation with acid permanganate, the resulting colour being extracted with a mixture of amyl alcohol and amyl acetate. 'Colour' was estimated in relative units, using diluted whisky as a colour standard. Electrical conductivity (expressed as reciprocal megohms per centimetre cube at 20°C) was determined with a commercial (Evershed and Vignoles' "Dionic Water Tester") conductivity meter, and alkalinity due to bicarbonate and carbonate by titration with N/50 HCl to pH 4.5. Carbon dioxide was estimated indirectly from alkalinity and pH (Moore, 1939); the results are reliable only where other free acids are absent. Dissolved oxygen was measured by Alsterberg's (1926) modification of the Winkler method, the samples being collected by a Ruttner sampler from which water temperatures were also read. Values for percentage saturation are based upon the data of TRUESDALE, DOWNING & LOWDEN with correction for altitude (MORTIMER, 1956). Colorimetric analyses were made using a B.D.H. Lovibond 'Nesslerizer' or 'Comparator' with coloured glass standards, the latter being calibrated against standard solutions.

Transparency was determined with a standard Secchi disc of 30 cm diameter. Light penetration was measured with an underwater photometer incorporating a selenium rectifier photocell and red, green and blue glass colour filters (numbers OR1, OG9, and OB10 manufactured by Chance Bros.). Care was taken to avoid errors due to the curvature effect in the photocell response at high light intensities (cf. Atkins et al., 1938). The results are given as mean values of the vertical extinction coefficients (defined, for example, by Sverdrup, Johnson & Fleming, 1942) for the various cell-filter combinations. The optical centres of gravity of these combinations during measurements were estimated at wavelengths of approximately $460 m\mu$ (blue), $560 m\mu$ (green), and $625 m\mu$ (red).

All the analyses given refer to samples of surface water. These are considered to be representative, as temperature stratification was usually slight or absent, and occasional analyses of surface and bottom water showed no noteworthy differences. An exception exists for the lower reservoir region, which shows an intermittent stratification

that will be described in detail elsewhere.

THE INFLUENCE OF VARIOUS DRAINAGE BASINS

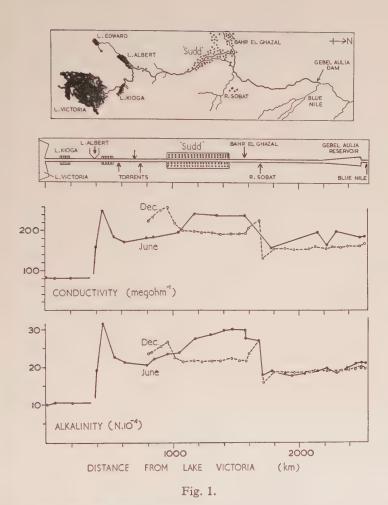
Changes in various water characteristics along the river are shown in figs. 1-5, each variable being plotted against distance by river from Lake Victoria. The river course is illustrated by an outline map (fig. 1), and by a linear diagram which is repeated in all figures so that the positions of the tributaries and swamp regions can be readily located.

The influence of a tributary water can be expected to be related to the volume and distinctive character of the water contributed. On these grounds four contributions – from Lake Albert, several torrents 380-760 km from Lake Victoria, the Bahr el Ghazal river system, and the River Sobat – are noteworthy. Measurements of their water characteristics (excluding the torrents for which data are not available) are given in table 1. Although the Bahr el Ghazal water shows several distinctive features (eg. high transparency and silicon content) its discharge is too small to modify significantly the properties studied in the main river. In its upper stretches the pH falls considerably, and a rich Desmid flora exists there (Rzóska et al., 1955).

TABLE 1
Water characteristics of three tributary waters, measured shortly before their junction with the main river.

	L.Albert	Bahr el Ghazal	Sobat
Date of sampling	27. v. 54	30. xii. 53	10. xii. 54
conductivity (megohms-1 at 20°C)	675		112
alkalinity (N. 10-4)	81.6	21.4	15.2
pH	9.0	7.8	6.8
dissolved oxygen, mg/1	_	-	3.4
% saturation	_	direction in the last of the l	44
$NO_3.N (mg/1.)$	0.04		0.015
$NH_3.N (mg/1.)$	-	0.1	0.02
$PO_4.P (mg/1.)$	0.18	0.02	0.045
Si (mg/1.)	0.6	18	12
C1 (mg/1.)	18	< 2	< 2
Ca (mg/1.)	9.0		8.7
SO_4 (mg/1.)	_		<1.5
transparency (m)		1.2	0.35

The contribution from Lake Albert, based upon drainage from the western Rift Valley, has probably the most profound effects. The high levels of total salts (cf. conductivity), alkalinity, pH, phosphate, sulphate, and chloride in the lake, compared with those in the inflowing Victoria Nile, lead to marked increases in these quantities downstream in the Albert Nile. This enrichment is especially notable



Outline map and schematic representation of the White Nile and adjacent waters, with swamp regions indicated by stippled areas; in the two lower graphs the variation in electrical conductivity and alkalinity along the river is shown.

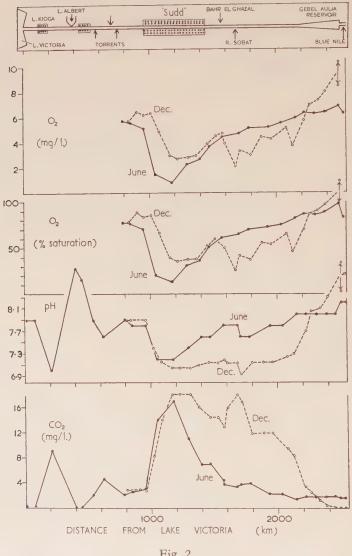


Fig. 2.

Variation in dissolved oxygen, pH, and carbon dioxide (calculated from pH and alkalinity, see p. 75) along the White Nile. At one station the daily range for oxygen and pH is shown by vertical arrows.

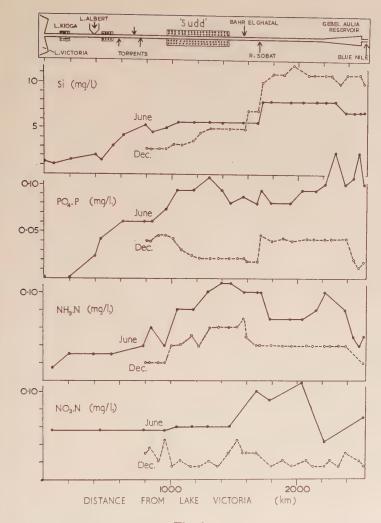
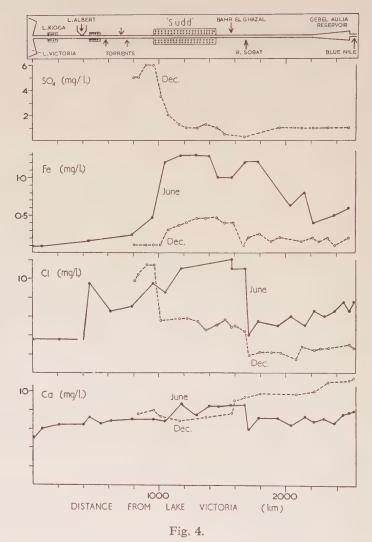


Fig. 3.

Variation in the plant nutrients silicon, inorganic phosphate, ammonia, and nitrate along the White Nile.



Variation in sulphate, total iron, chloride, and calcium along the White Nile.

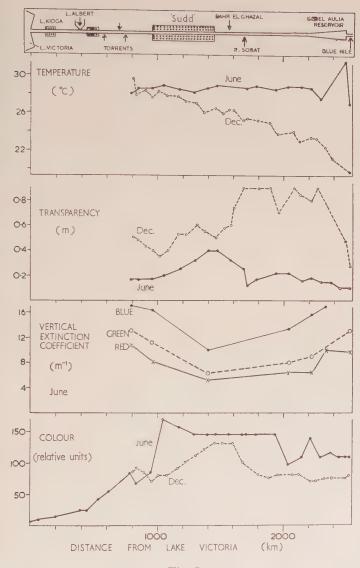


Fig. 5.

Variation in some physical quantities, surface temperature, transparency (from Secchi's disk), vertical extinction coefficients, and colour, along the White Nile. The values for colour are not directly comparable between the two seasons.

for the plant nutrients phosphate and (according to Dr G. R. Fish, private communication) sulphate, whose contents downstream appear to be almost entirely derived from the lake. The effects of Lake Albert are however complicated by the possible occurrence of large yearly fluctuations in some constituents (Anon, 1954), and by short-period variations in the volume of its contribution (Hurst, 1925; Tottenham 1926: Newhouse, 1939, p. 27). The latter variation is reflected in large fluctuations of the conductivity of samples collected weekly in the river just below the lake (Beauchamp, 1956). It also accounts for local maxima of conductivity, alkalinity, and chloride discovered in the river some 60 km below the lake (1 May 1954) and 375 km below (December 1954). The last mentioned maximum had vanished when the river region affected was resurveyed in January 1955. It appears unlikely that these temporary fluctuations have any biological significance in the river, except possibly close to the lake.

The tributary torrents, which enter the main river some distance below Lake Albert, have not been examined as to water characteristics. Consequently their influence is less easily demonstrated, but almost certainly includes an enrichment in dissolved silicon (fig. 3) and decrease in transparency (noted subjectively) that occur in this region. The silicon content and the turbidity below these tributaries near Juba (750 km from Lake Victoria) were much higher in June than in December, as would be expected from the seasonal flow of the

torrents (Hurst, 1952, fig. 17).

The River Sobat, the last important tributary, also produces considerable modifications in the main river. These include the decrease of conductivity, alkalinity, chloride, and transparency; an increase occurs in silicon and (during the December observations) phosphate. The Sobat discharge also shows a large seasonal variation (Hurst 1952, fig. 17) which probably underlies several differences between the June and December series. A seasonal variation in the composition of the tributary water is also likely, although data are not available. At high water much Sobat water passes through parts of an adjoining swamp system, the Machar marshes. Their influence may account, at least in part, for the depressed levels of oxygen and pH found during December in the Sobat and in the main river below.

THE INFLUENCE OF RIVERAIN SWAMPS

Riverain swamps are well developed in three areas (fig. 1) within which modifications of varying degree occur in the river water. In the shallow Lake Kioga, 125 km from Lake Victoria, a dense cover of water-lilies (Nymphaeaceae) exists over much of the water surface.

In addition fringing swamps, which include abundant papyrus (Cyperus papyrus L.), are extensive. Further swamp regions exist along the river stretch (385-540 km from Lake Victoria) immediately below Lake Albert, and in much greater development in the southern Sudan (1000—1500 km from Lake Victoria). The latter swamp region (the 'Sudd') has an estimated area of about 8000 km² and extends about 500 km along the river. Large parts are dominated by Cyperus papyrus, although grasses (especially Echinochloa stagnina P. Beauv. and Vossia cuspidata Griff.) are also important. The vegetation is described by Migahid (1947) and the Jonglei Investigation Team (1954). Important features of the swamp in the present connexion are the large loss of water (about half the river inflow) and the seasonal inundation of marginal land ('toich') by changing water levels. Within parts of the swamp area the river is split into several channels, whose size varies with season.

The influence of swamp conditions upon river-water characteristics was strongest, and was studied in most detail, in the large Sudd region. Here processes of decomposition caused a fall in dissolved oxygen and pH, the latter being interpreted as the result of a corresponding increase in carbon dioxide (fig. 2). The deoxygenation was much more strongly developed in June than in December. The causes of this change need more investigation, but may be connected with the displacement of swamp water by changing water levels or by the rains mainly present between April and October. An effect upon oxygen exchange from diurnal changes of thermal stratification may also be involved, as discussed for other tropical swamps by CARTER & BEADLE (1930), BEADLE (1932a), and CARTER (1934, 1955). Seasonal oxygen depletion may well be the cause of a large mortality of fish which usually occurs in this region each year about July and September.

The behaviour of several other quantities may be connected with that of oxygen. Total iron, for example, increases sharply in the swamp region owing to the solubility of ferrous iron formed under reducing conditions. The increase is greatest in the more reducing conditions of June. Inorganic phosphate shows different behaviour in the two seasons, with some increase in the swamp region during June but a marked reduction during December (fig. 3) and January. The decrease may arise from adsorption on the surface of mud under more oxidising conditions then prevailing, as is well known for muds bearing a film of ferric hydroxide. Removal of phosphate from river water flowing through a tropical swamp has also been demonstrated by BEADLE (1932b, pp. 194-6) for the Chambura river in Uganda.

The December observations showed a striking removal of sulphate soon after the river water had entered the swamp region. Less detailed measurements by Dr G. R. FISH (private communication) suggested a similar situation in June. There is good agreement with earlier observations, in 1904 or 1905, by BEAM (1906). The activity of sulphate-reducing bacteria under conditions of oxygen deficiency is presumably responsible. The concentration of sulphate in the water leaving the swamps was too low (under 1.5 mg/1.) to be determined accurately with the method used.

Swamp conditions would also be expected to modify the concentrations of ammonia and nitrate nitrogen in the river water. A noticable rise in ammonia was present in both the June and December series. Nitrate appeared to be less affected, although an irregular fall is suggested in the December series. The levels of both ammonia and nitrate nitrogen were higher in June than in December, but the difference appears largely due to changes higher up the river. In neither season were nitrites detected.

The high evaporation losses within the swamp region would be expected to increase the concentration of total salts, with which conductivity and alkalinity are closely correlated. Such increase is apparently present in the June but not the December series, although evaporation losses in the latter season are still considerable. Other modifying factors may have obscured the effect in December; the influence of oscillations in the contribution from Lake Albert has been already mentioned (p. 82).

The interpretations given above are supported by analyses of swamp waters some distance from the main river channel. They were taken in June 1954 from two points in the *Sudd* swamps 950 and 1460 km from Lake Victoria: at the first a transect was made across a marginal swamp. These swamp waters showed modifications generally parallel to – but more marked than – those found along the main river, particularly decrease in oxygen and pH and increase in ammonia and total iron. No direct evidence is available on the question of seasonal changes.

Fewer data exist for the two remaining large swamp regions, which were visited in June only. There is in both, as in the *Sudd*, a fall of pH and a corresponding rise of free carbon dioxide in the river water. Changes in ammonia, nitrate and total iron appear slight or absent; dissolved oxygen was not measured.

The figures show that some of the modifications in the swamp regions are local (eg. of oxygen in the Sudd) whereas others persist for considerable distances downstream (eg. total iron and sulphate below the Sudd).

DISCUSSION

Many characteristics previously described are of importance for plant growth. Their modifications in the river are summarized below from this viewpoint, with particular reference to phytoplankton requirements. In this river section dense populations of phytoplankton have been found only in the lowermost reservoir region near Khartoum (Brook & Rzóska, 1954; Rzóska, Brook & Prowse, 1955). Further upstream densities are very low, except in local waterbodies (eg. lagoons) off the main river (Prowse, 1954). This feature is remarkable in view of the many planktonic algae entering the river from lakes Victoria and Albert, and the appreciable time of flow (as deduced from the time of travel of hydrological disturbances) which averages about 35 days between Lake Victoria and the head of the reservoir region (Morrice, 1956).

Of physical factors, temperature (fig. 5) is unlikely to modify directly the distribution of phytoplankton in the river. The temperature range in June was small (27-32°C), although in December there was a decline northwards from 30° to 20°C. Larger seasonal changes in the Gebel Aulia reservoir could not be correlated with the growth of phytoplankton there (Prowse & Talling, in prep.). Light penetration (fig. 5) would appear of greater significance, since the relatively high absorption (and hence extinction coefficients) recorded imply a correspondingly shallow photosynthetic zone. The minimum extinction coefficient over the spectrum may be taken as the best single measure (TALLING, 1955, 1957). Values of 1.5 to 3.5 (per metre), with corresponding photosynthetic zones of depth 2.5 to 1.2 m, were found in the reservoir region during October 1954 and 1955 at times of active phytoplankton growth there. Such growth may not be possible under the higher minimum extinction coefficients (c. 5 to 10) measured in the upper river region during June 1954 (fig. 5). However the situation is complicated by varying river depths and by the seasonal variation in light penetration indicated by the transparency data. It can be concluded that regional and seasonal changes in light penetration undoubtedly influence greatly the conditions of growth for phytoplankton, although an absolute limitation of growth is difficult to establish.

Of the major inorganic plant nutrients, phosphate shows a very varied history in the river. The low levels derived from Lake Victoria are suddenly increased by the contribution from Lake Albert, so that relatively high concentrations are characteristic of the later river sections. Modifications appear to be imposed by seasonal removal in the swamp region and during the growth of phytoplankton in the lower reservoir region. It is possible, though uncertain, that the latter

depletion may limit the growth of certain planktonic algae (Prowse & Talling, in prep.). In any case the seasonal variation of phosphate phosphorus in the productive reservoir region is remarkably high,

from under 0.003 to about 0.2 mg/1.

Unlike phosphate, inorganic nitrogen (as ammonia and nitrate) appears always in low concentration, although some seasonal and regional variations have been described. In these, swamp effects appear to predominate, although extreme modifications have been not found. There is some direct evidence from cell analyses (PROWSE & TALLING, in prep.) that the low concentrations may limit the densities attained by the dominant diatom of the reservoir, *Melosira granulata* (Ehr.) Ralfs.

Dissolved silicon is another nutrient which enters in relatively low concentration from Lake Victoria and is subsequently enriched by tributary waters (here the torrents and the River Sobat). During most of the year its concentration in the reservoir region is 7—11 mg/l., and never falls to the low levels (under 0.25 mg/l.) found elsewhere to limit the growth of plankton diatoms (cf. Lund, 1950). It appears, however, that there may be an appreciable reduction during the

growth of Melosira in October.

Water from Lake Victoria also contains sulphate in low concentration (c. 0.8—1.8 mg/1.; Beauchamp, 1953), and the higher values (near 6 mg/1.) found downstream in the south Sudan are largely due to the contribution from Lake Albert (p. 82). These values are soon dramatically reduced by the *Sudd* swamps to low concentrations under 1.5 mg/1., which persist along the lower river. It is not known whether these concentrations fall to the levels below 0.5 mg/1. suggested by Beauchamp (1953) as limiting phytoplankton growth in other African waters.

In general, it seems unlikely that the physical and chemical features described above can account for the small development of phytoplankton above the reservoir region, compared with its great development in the reservoir during storage of water there. However, a good correlation was found between phytoplankton development and the slowing down of the current in the reservoir section. Current velocities measured at various points above the reservoir, 1400—2000 km from Lake Victoria, generally exceeded 0.5 m/sec. In the reservoir region during storage in October 1954 the velocities declined from about 0.35 m/sec to under 0.1 m/sec near the dam, so providing additional time for algal growth. It is evident, however, that the total time available for algal development between Lake Victoria and the reservoir head is still considerable, and other factors may well be involved in this upper stretch.

Little comparison can be made between longitudinal succession in

the White Nile and that in other large tropical rivers, as the latter seems little known. In particular the changes in a tropical river traversing a large swamp region have been little investigated. The *Sudd* swamps described here act in some ways as a giant filter or exchange system, and the seasonal changes in their effects would repay more detailed study. Succession in the rivers of the Amazon system (Sioli, 1951) appears different in many respects, particularly in the transition between turbid 'white water' rivers and the more acid 'black water' rivers affected by drainage from podsolic soils.

SUMMARY

The longitudinal succession of physical and chemical water characteristics in the White Nile is described, and some seasonal differences are outlined. Most successional changes are due to tributary contributions, of which the discharge from Lake Albert is particularly important, and to riverain swamps, especially in the south Sudan. Swamp effects include a partial deoxygenation and depletion of phosphate and sulphate, of which the first two vary considerably with season. The origin and extent of changes in plant nutrients, and in physical factors affecting plant growth, are discussed with reference to the growth of planktonic algae in the lower river region.

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